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NOTES ON THE BREEDING BEHAVIOR OF THE ANHINGA

TED T. ALLEN

LITTLE information has been published on the breeding activities of the Anhinga (*Anhinga anhinga*) in spite of its rather common occurrence in many places in the warmer parts of the United States. The literature on behavior and life history of this species has been limited to accounts of a few isolated observations. The present paper reports some behavior not previously presented in the literature, and it is hoped that this information will be of value in further behavior studies of this species.

These observations were facilitated by the convenient location of a nesting area at Lake Alice, which adjoins the southwestern portion of the University of Florida campus in Gainesville. The easy accessibility of the area, along with the occurrence there of a breeding colony composed of nearly a dozen water bird species, makes it a valuable location for field work, especially in behavior.

Behavior of pair formation was the primary subject of study, although comments have been included on other activities. Behavioral sequences have been generalized from observations of many birds in various stages of reproductive activity at Lake Alice during the breeding season of 1959.

METHOD

All observations were made from the shore or from trees around the lake. Such a study was feasible since many of the nesting birds were close to the shore and in relatively exposed locations. Because of the great disturbance involved to heavily concentrated heron and ibis colonies, which were the subject of another study in progress, no attempt was made to go out into the lake, and therefore no close observations were made on the nests, eggs, or young. Nevertheless, with 10× binoculars and a variable-power telescope, observations could be made on the behavior of birds in the area, most of which seemed undisturbed by quiet human activity.

STATUS AND HABITAT

Most of Lake Alice is actually swamplike with various trees standing dead or growing in shallow water. Less than half the area is strictly open water. Anhingas are permanent residents in the swamp habitat of the lake (Karraker, 1953), but more are present during the breeding season than in the winter. The first territorial and courting behavior was observed on 20 March, and this continued until the study ended in late May.

Lake Alice, in spite of its proximity to concentrated human activity, serves as a nesting place for thousands of water birds of several species. The most abundant of these in 1959 was the White Ibis (*Eudocimus albus*).

In the breeding season of 1952 Karraker (1953:29) estimated the population at 2,500 individuals. Other birds which were numerous, but in lesser concentrations, were as follows:

Glossy Ibis (*Plegadis falcinellus*)
Cattle Egret (*Bubulcus ibis*)
Snowy Egret (*Leucophoyx thula*)
Little Blue Heron (*Florida caerulea*)
Common Gallinule (*Gallinula chloropus*)
Purple Gallinule (*Porphyrula martinica*)
Red-winged Blackbird (*Agelaius phoeniceus*)
Boat-tailed Grackle (*Cassidix mexicanus*)

Anhingas nested in two colonies, both composed of mixtures of all the above species. Karraker (1953:22) estimated the total Anhinga breeding population to be approximately 100 birds, and my estimate in 1959 was about 60, although an accurate census from the shore was quite impossible. In one of the colonies Anhinga nests were located in some dead trees, about 55 feet tall and about 100 feet from the southwest shore of the lake. The nests were located from about 5 to 25 feet above the water and placed no less than 8 feet apart. Anhinga nests in the other colony were located in small red maple (*Acer rubrum*) trees standing within 150 feet of the middle of the south shore of the lake. These nests varied from about 8 to 15 feet above the water, and most of them were located near the tops of the small trees. Usually the nests appeared to be separated from each other by at least 15 feet, but one nest was only about 2 feet below another one in the same tree.

EXTERNAL FEATURES

A male Anhinga in full breeding plumage is mostly black, glossed with green. It has developed a mane, not present in the winter, which is comprised of decomposed black feathers on the hind neck which become grayish brown on the crown and sides of the neck (Brodkorb, 1957). This mane is often erected in sexual displays. The area around the eye is an iridescent blue and green which changes to yellowish on the lores, and the effect of this bright color emphasizes the eye. The greater coverts appear as a patch of silvery feathers on each side when the wings are folded, and the scapulars and tertials are also streaked with silvery.

The female is fawn-colored on the head, neck, and upper breast and has a somewhat smaller and lighter-colored mane than the male. Also present on the female is a black mark beginning on the rictus and extending down into the gular sac. With such marked differences in the appearance of the head, neck, and upper breast of the two sexes, it seems reasonable to assume

that sex recognition is at least partly visual. In other details the sexes are generally similar.

PRELIMINARY NEST AND EARLY DISPLAY

In the latter part of March the Anhingas began concentrating in the area, and their early activity was characterized by much shifting about. In mid-March there were a few consecutive days of rainy and cloudy weather, during which time nothing was observed which indicated breeding activity. On 20 March the weather cleared, and there was a rapid initiation of display behavior. Pairing occurred rather rapidly during the following three days, but I had little chance to visit the area during that time. There subsequently was an almost regular occurrence of new birds on the lake, however, and the behavior of these was closely studied.

The male apparently takes over an old nest, if one is available, and establishes his territory there. Bent (1922) reported that the birds return to the same nest each year, but this seems doubtful at Lake Alice, considering the hundreds of birds of several species which might take over old nests or confiscate materials from them. (A Snowy Egret was seen repeatedly pulling sticks out of an old unidentified nest and carrying them to its mate, which was building a nest.) Furthermore, no Anhingas nested within 50 yards of the location of a breeding colony in 1958. Four people, all familiar with the lake, separately informed me of this location. It seems generally known, also, that the Lake Alice colonial birds shift the locations of their nesting sites from year to year. No good explanation for these shifts is available, but they may be influenced by the supply of nesting material, which certainly is subjected to great local reductions during each breeding season.

Male Anhingas did not always take over old nests, although most of the earliest ones apparently did so. Each male which arrived on the area after all old nests were occupied gathered rather long, coarse sticks and arranged them in a flattened clump which I have called the preliminary nest. Only once did I actually see a male carrying sticks to one of these nests, but the regular occurrence of them in previously bare places, and their subsequent occupation by single males, indicates that males built the structures. These nests were later elaborated by the male and female, after pair formation, and were eventually used for nesting. The final arrangement of the nests within the colony was therefore determined by the arrangement of the preliminary nests.

After the male establishes himself on a nest, he begins an invitational display which starts with a wing-waving performance. This behavior is mentioned by Karraker (1953:23) and briefly described by Meanley (1954: 83). The following is a generalized description of the performance. The

male stands in the nest or on a nearby branch and raises and lowers each wing separately, still otherwise folded, at the rate of about 3.5 beats per second. While one wing is fully raised the other is held in the normal resting position against the body. As one wing is raised the other is lowered. Each wing is raised upward and slightly outward away from the body so that at its extreme point of movement it forms an angle of about 30° with the long axis of the body. Frontispiece (1) shows a male in a common perching posture, and Front. (2–4) show some of the postures assumed during wing-waving. The neck is sometimes held in an S-curve and sometimes in a tight inverted-U-curve with the head flat against the base of the neck. During wing-waving the mane is sharply erected, and the tail is sometimes raised. The neck often has a thickened appearance caused by its tight retraction and the stretching of the loose flesh on its ventral surface. After a variable period of wing-waving (usually 5–15 seconds), the male makes a deep bow. In doing this the wings are held out from the body, the neck is held in a tight inverted-U-curve, and the tail is erected and spread (Front. [5]). This display usually lasts only about four seconds, during which time the wings are vibrated very slightly but very rapidly. After the bow the male ruffles his wing and back feathers and then resumes wing-waving.

The wing-waving produces a flashing effect of the silvery patches on the wings, and this seems to serve to attract the attention of passing females. The movement certainly made them more noticeable to me, because I was often able to find males which were partially obscured by foliage, only because of these flashing wing patches.

The wing-waving and bowing behaviors occurred at various times during full daylight hours, and no predominance could be seen at any one time of day. Usually, quiescent males began the display when a female came into sight, but most males wing-waved and bowed even when there apparently were no females near.

DISPLAY VARIATIONS AND FEMALE BEHAVIOR

Occasionally in April, and somewhat more often in late May, male Anhingas were seen wing-waving and bowing from bare branches. These birds apparently had not established preliminary nests. They often moved toward any female which came near, whereas the males on preliminary nests in the same area remained on the nests. I never saw a female tolerate such an approaching male, however, and her nearly invariable reaction was to move away. Meanley reported some similar observations on these apparently non-territorial males.

Unattached females made short, wandering flights through the areas where males were displaying, and often they paused for several minutes watching particular males. A female seldom showed any response except some slight

stretching and retracting of her neck, and after a time she moved on to another male (or out of sight).

When females began wandering through areas where there were males, both with preliminary nests and without, complex interactions sometimes occurred. The following is an example of one such situation:

A female was seen giving a slight response (slight neck-stretching and retracting) to a male displaying below her on a preliminary nest, and also to a displaying male on the same branch with her; this latter male was without a nest. The male on her branch moved toward her, but then he suddenly flew off to another female. Very soon he flew back again to the first female, whereupon she flew out of the tree and landed in a bush close to an Anhinga nest in which there were downy young. The female from the nest came hopping across the branches, with wings outspread and bill opened, toward the female which had just landed, and the latter retreated out of the bush. The fleeing female then flew to another bush, closely followed by the male which had previously been on the same branch with her. The new bush had a male in it, however, and he moved out and drove away the male which had followed the female. The remaining male then began to display to the female, but she soon flew out of the bush and out of sight.

PAIR FORMATION

The next type of male display usually occurs when a female approaches, although it may appear mixed with wing-waving and bowing. Sometimes a female will remain near a wing-waving male and react with slight extensions and twistings of her neck. These actions seem to be of low-intensity response and actually appear to be little more than an attempt by the female to change her view of the male. These actions may not constitute the stimulus for the change of display by the male, but when a female begins them, or moves closer, the male begins to stretch his neck and move it in wide sweeping arcs. The most common direction of movement is downward with the neck bending only near the body and the head and bill being held in line with the extended neck (Front. [6–7]). Sometimes the male assumes such postures with the bill pointing directly toward the female and with the mane and tail erected and the gular sac expanded. He usually holds these positions for four or five seconds with only a slight bobbing movement of the head. He then draws back his neck, ruffles his feathers, and extends his neck again. A further variation of this behavior is seen in the slight elevation of the wings (Front. [6]) and sometimes in the grasping of a leafy twig (Front. [8]). Usually the male performs the latter only when the female continues to respond and approaches the male, although once a male without a preliminary nest was seen to perform this action after he had approached a female. While the male grasps the twig he makes vigorous and rapid sideways movements of the posterior part of his head and upper neck, but no male was seen to break off a twig in this manner. Hotchkiss

(1954) reported a male breaking off two willow branches and presenting them to the female, apparently during this same phase of courtship.

By this time some changes in the behavior of the female become obvious. She opens her bill and rapidly vibrates her throat, while the sweeping movements of her head and neck become more pronounced and very similar to those in the male, including the pointing posture. She continues to move closer to the male until her neck appears to be crossed over the neck of the male. The two birds often remain for five seconds or longer with the necks held stiffly straight and crossed, or in positions similar to those shown in Front. (9). Various other stiff-necked sweeping movements are made with the head by both sexes.

Several additional behavioral responses now begin to appear. The male may perform a rapid wing-waving, at least twice as fast as the early invitational type. This occurs interspersed among neck movements, display bows, and feather rufflings. It is common at this stage to see the male with his neck extended nearly vertically and with a flattening of the flesh of the throat laterally, which gives the neck a thickened appearance from the side view. The female then responds with a bowing identical with that of the male, and sometimes they bow in unison. The birds then begin mutual preening and bill-rubbing movements (Front. [10]), and finally the male inserts his bill into the throat of the female in what seems to be mock feeding (Front. [11]). This may precede copulation and may also recur later.

When the mock-feeding performance was first seen, it appeared to be agonistic behavior. This impression was created by the shifting positions of the two birds and by vigorous and rapid side-to-side movements of the head of the male while his bill was inside the throat of the female. It was not possible to observe whether any food material was actually passed between them.

Copulation soon follows after the female steps onto the nest and begins answering the feather ruffles and bows of the male with similar gestures. Sometimes the male walks out on a branch a few feet away from the nest and ruffles his feathers, wing-waves, and bows. The female answers these gestures, and the male hops directly back to the nest and plants both feet on the upper back of the female. She makes little response other than the lowering of her extended neck. The male then grasps the bill of the female and pulls her head upward and backward, and both partially spread their wings and tail. Next the male lowers himself to the female, and copulation occurs, with many movements of the wings and tail of both birds. The duration of copulation is about five seconds.

After the first copulation the pair resumes the posturing which just preceded mating, and the male may again move away from the nest, display, and quickly return to attempt to copulate with the female, not always suc-

cessfully. This sort of behavior continues for several days following the first copulation, and the pair bond certainly seems to be firmly established since the first mating. Copulation and its associated behavior diminish in intensity and frequency after the first day and are rare by the fourth day.

Since the preceding is largely a generalized account, it does not give details of overlappings and variations of the actions. Some parts of the sequence, such as the initial entrance to the nest by the female, and copulation, were observed only two or three times. I think, nevertheless, that the general pattern was repeated closely enough to allow accurate generalizations.

The recent publication by Meyerriecks (1960) on breeding behavior in herons allows some general comparisons with Anhinga behavior. (The following page references are from Meyerriecks.) A difference was noted in the early stages of pairing. The initially hostile response of a male Green Heron to an approaching female (p. 76) was not seen in the Anhinga, although the neck-stretching displays (Front. [6–7]) were similar to the few hostile attitudes which were observed and could perhaps have evolved from them. Aside from phylogenetic considerations, this type of behavioral difference might be expected on the basis of the easier sex recognition afforded by the more pronounced dimorphism of the Anhinga. Certain similarities were noted between the Stretch Display (p. 43) and Snap Display (p. 33) of the Green Heron to the behavior of the Anhinga shown in Front. (6–9). Feather-nibbling (p. 34) and Billing (p. 51) as well as movement of the male in and out of the nest before and after copulation (p. 52) were very similar in the two species.

NEST BUILDING

The process of finishing the nest is begun soon after pair formation. Sometimes within 20 minutes of the first copulation the male begins to make short trips to surrounding bushes to bring sticks and twigs which the female incorporates into the nest, apparently by wedging them in with thrusts of her bill. There seems to be no set ceremony involved in the transfer of a twig from the male to the female. A female was once seen to open her bill and shake her head from side to side as the male approached with a stick, and she seemed to preen him briefly as he came to the nest. At another time a female was seen to do the neck-extended bow (Front. [7]) just before taking a twig from her mate. All the gathering seems to be done by the male, as Meanley reported, and the female does not help even when her mate is collecting twigs within easy reach of the nest.

Nest building continued for at least three days after pairing in all the birds that were observed, but Meanley reported that nests may be completed in one day. Variability in time taken for nest completion may have been

caused by differences in the availability of material, and it may have been influenced by the condition of the preliminary nests. As the female (and sometimes the male) wedges new sticks in among the old ones, the structure becomes considerably enlarged. The completed nests appear to be lined copiously with leafy willow twigs, which show around the rim. The willow of the area is *Salix longipes*, and Anhinga males were seen collecting its branches.

There was good indication that the females stayed at the nest constantly during the first few days after pairing. Complete observations of the pair formation were made at two nests, starting from the solitary wing-waving of the male. After pairing, the female of one was seen in the immediate vicinity of the nest, each time it was observed, for eight days immediately following pairing. Not until the ninth day was she gone. The other was seen on the nest on each of six consecutive days, but no observations were made in the next three days. Once a very wet-appearing male returned to one of these waiting females, and he appeared to feed her. Before the feeding the female performed what appeared to be a display bow with partially opened wings and a spread and erected tail. The male then inserted his bill into her throat and moved his head rapidly from side to side.

The implication from these observations is that the female stays on the nest and is fed by her mate during the first few days after pairing. Even if she occasionally leaves the nest, her presence there is much more nearly permanent than that of the male. The presence of a bird on the nest at all times conceivably could prevent other birds of the colony from taking over the nest or taking its materials.

During the collection of nest material and foraging for food for the young, the birds would usually fly in and out of the nest tree and only occasionally would they climb up out of the water into the tree without flying. Apparently most foraging was being done in the open-water section of the lake or in another lake about one-half mile away. This predominance of flying to and from the nest, instead of swimming and climbing, may be a characteristic behavior for this particular habitat and may not occur in other areas (as indicated to me by Dr. Oscar T. Owre of the University of Miami).

INCUBATION

Incubation is certainly by both sexes as reported by Bent (1922), but no indication was seen that the female does the greater share, as he reported. In my notes there are records of males incubating 13 times and females 16 times. These represent only a small portion of the incubating birds actually observed, however.

No particular ceremony or noteworthy behavior seems to be involved in nest relief. The incubating birds sit usually with mouth opened and throat

rapidly and shallowly inflating and deflating, especially during the warmer parts of the day. Incubating birds may also be observed, at intervals of several minutes, to make slight changes in the direction in which they are facing; the total effect of these movements is one of a slow rotation inside the nest.

INTRASPECIFIC RELATIONSHIPS

The general arrangement of the nests within the colonies has already been described. The colonial groupings of nests indicate that territories are small, but there was never enough interaction among the Anhingas to allow determination of territory boundaries. I have seen two males wing-waving in the same bush, but I have twice seen a male chase another one out of the bush where the former was displaying. One of these occurrences was previously cited, and both incidents involved the presence of females, which might have caused an increase in the aggressiveness of the males. Once two males were seen bowing and pointing to each other from a distance of about 15 feet, in a manner exactly like that described for the pointing display in pair formation (Front. [7]). Generally the males showed little response to the presence of other males, and paired males allowed close encroachment by wing-waving males. This sort of tolerance seems necessary for establishment of the compact nesting groups, although the infrequency of territorial interaction is in sharp contrast to the high frequency of border-clashes noted in the early establishment of Green Heron territories (Meyerriecks, 1960:62).

The only observed instance of nest defense was a response to the only observed encroachment upon a nest. This particular trespass, discussed above, seemed accidental.

INTERSPECIFIC RELATIONSHIPS

In both Anhinga colonies there were many nesting ibises and herons. In the colony which was in the maples the concentration was heavy. Some Anhinga nests were in the same bush with White Ibis and heron nests, but in some bushes there were only Anhingas. Once a returning male Anhinga flew into what may have been its preliminary nest or an incomplete ibis nest, in the midst of a group of several White Ibises. This caused considerable shuffling of the ibises, but then the Anhinga stood on the nest and pointed to them with extended head and neck in what apparently was a threat display. His wings were held open, and he made long thrusts with his bill, but the ibises quickly moved out of range. At another time a male Anhinga moved from a bush where he had been displaying to a bush closer to a female. He chased a White Ibis from a nest in this bush and climbed up on the nest to display to the female, which soon flew away.

Twice, however, Anhingas were seen to ignore the close proximity of ibises. Once a White Ibis landed within two feet of a paired male Anhinga without either showing any response to the other. Another male Anhinga,

also showing no reaction, was observed sitting in the midst of a group of White Ibises. This ibis was the only species which showed any interaction with the Anhingas.

VOCALIZATIONS

One of the major difficulties with this type of study was the impossibility of studying sounds and calls made by the Anhingas. Audubon described rough, guttural sounds and whistling notes, and Meanley (1954) mentioned notes similar to those of a Screech Owl (*Otus asio*), but I could detect none of these. The distances involved combined with the continuous series of raucous noises from the other inhabitants of the lake made it quite impossible to detect any sounds that could be traced to the Anhingas.

SOARING

During the late winter and early spring particular attention was given to the soaring behavior of the Anhingas to see if it had any relationship to reproductive activity. Bent (1922) quotes a passage from Audubon which mentions "courting on the wing" in Anhingas, which may have been based on the soaring. Many individuals and groups of birds were observed soaring, but there was no indication of any sexual significance.

The birds engaged in soaring as early as 13 February and perhaps all through the winter. The general pattern was for the birds to rise in tight circles, with alternate flapping and gliding, until favorable air currents allowed them to gain altitude without the wing beats. Often the birds would be difficult to follow, even with 10× binoculars, at the height of their ascent. At times I suddenly lost sight of the birds in the sky. Bent (1922) tells of abrupt diving at the end of a soaring flight, and this may account for the disappearances, although I never observed it. At other times birds would droop their wings slightly and lose altitude in a long, slow descent.

The composition of the soaring groups offered no hint of the meaning of the behavior. The groups would usually include both sexes, of varying proportions, and number up to as many as 11 birds. It was not rare, nevertheless, to see a bird circling by itself, and once a male Anhinga soared for about five minutes in close company with a Double-crested Cormorant (*Phalacrocorax auritus*). Although the members of the soaring groups usually circled close together, no interaction could be detected.

SUMMARY

This study was made at Lake Alice in Gainesville, Florida, where Anhingas breed in close association with ibises and various herons. The behavioral sequence of pair formation is generalized from observations of breeding birds during the late winter and spring of 1959.

Anhinga sexual dimorphism is shown by the fawn head and neck of the female compared with the glossy black coloring of these parts in the male. The male has a mane which is conspicuously erected during sexual displays.

The male either takes over an old nest or builds a new "preliminary" nest, on which he stands to wing-wave, ruffle his feathers, and bow. The wing-waving flashes the silvery patches on the wings and probably serves to attract females. Females wander through the area occupied by displaying males and are occasionally pursued by non-territorial males.

If the wing-waving attracts a female, the male begins to change his behavior, employing sweeping movements of the head, rapid wing-waving, and pointing with the bill. The female approaches the nest and begins to answer the gestures of the male with similar ones. Copulation occurs soon after the female steps on the nest. After pairing, the male begins to gather sticks with which he and the female complete the nest. The female probably remains on the nest for several days after pairing, perhaps being fed by the male.

Incubation is by both sexes, and there seems to be no particular ceremony involved in nest relief.

Variability occurs in the defense behavior of territorial males, but reactions seem to be strongest when a female is near. Paired males are very tolerant of wing-waving males, a condition which allows establishment of compact nesting groups.

Anhingas seem to be generally tolerant of the presence of the other species of the colony, although occasional aggressive responses were observed. Herons, ibises, and Anhingas all nest close together, but interaction was observed only between the White Ibis and the Anhinga.

No observations were made on vocalizations of Anhingas. Soaring behavior was observed, but no relationship to reproductive activity was seen.

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DEPARTMENT OF BIOLOGY, UNIVERSITY OF FLORIDA, GAINESVILLE, FLORIDA, 29 JUNE 1960

SUMMER CREPUSCULAR FLIGHTS OF AMERICAN WOODCOCKS IN CENTRAL MASSACHUSETTS*

WILLIAM G. SHELDON

THE purpose of this paper is to record observations of American Woodcock (*Philohela minor*) during nine summers (1952–60) in central Massachusetts. Active primarily in crepuscular and nocturnal hours, this elusive upland shorebird has presented a challenge to those ornithologists or wildlife biologists seeking knowledge of its life history and ecology. Intensive study of this species by personnel of the Massachusetts Cooperative Wildlife Research Unit for ten years has included exhaustive summer investigations, a season when this species is difficult to find and secretive in habits. The dearth of information on woodcock summer activities during the crucial period of molting and rearing young prompted me to develop methods of gathering critical information. The results are based on 746 woodcock captures with Japanese mist nets. A detailed description of netting techniques appears elsewhere (Sheldon, 1960). Fragmentary and preliminary reports of these summer observations also have appeared elsewhere (Sheldon, 1956*b*).

Search of the literature reveals a paucity of data on the summer behavior of woodcocks. Pettingill (1936) reported that in quest for food during the summer months, woodcocks have been known to use haunts not frequented at other times of the year, such as lawns, cornfields, and vegetable gardens. Similar observations have been made during the course of this study. Mendall and Aldous (1943) suggested that in the heat of the summer and during the critical period of the molt, woodcocks retire to dense thickets where the soil is damp and productive of earthworms. Although most food studies indicate that earthworms form a high percentage of the woodcock diet, findings in this study suggested that other invertebrates play an important part in the woodcock's summer diet.

Evening observations during the summer months revealed a high degree of activity by woodcocks during the evening crepuscular period. Birds observed "trading" across country roads and elsewhere were pursued on the subsequent evenings if their flight direction appeared consistent. These investigations led to the discovery of certain fields where the birds alight. This phenomenon is not unlike descriptions of woodcocks coming into fields to feed for earthworms in their Louisiana wintering grounds. An elder sportsman told me of accompanying a market gunner during the last century when the Massachusetts woodcock season opened in July. He described

* This is a contribution of the Massachusetts Cooperative Wildlife Research Unit supported by the University of Massachusetts, the Massachusetts Division of Fisheries and Game, the U.S. Fish and Wildlife Service, and the Wildlife Management Institute.

dusk shooting of woodcocks flying to the slope of a dry hill in Essex County. Two small spaniels were used to retrieve the birds.

Exploration revealed four fields thus frequented at widely scattered locations in Quabbin Reservation which comprises 100,000 acres of protected land and water. Three of these were used as study and netting areas. Area 3 was open to the public and unsuitable for effective netting.

DESCRIPTION OF THE AREA

The ground of the frequented fields had little in common vegetatively. Such openings were bordered by trees or shrubs 20 feet or less in height, but grass or shrub cover varied in each area. Whatever the cover might be, there were a few relatively clear patches on the ground. Woodcocks appear to favor areas where they can walk around easily whether feeding or engaged in other activities. The only other feature in which these fields were similar was location in reference to spring breeding areas. All were in or very close to regions where the largest number of singing males was heard in the spring. All were used as singing grounds in the mating season.

Area 1.—One of the two areas where birds alight in Prescott Peninsula in Quabbin Reservation was a small field about ½ acre in size with a ground cover of low bush blueberries (*Vaccinium pennsylvanicum*), scattered sweet fern (*Myrica asplenifolia*), and a few clumps of oak (*Quercus* sp.) and chestnut (*Castanea dentata*) sprouts. There were open areas between the bushes which were the favorite alighting places. It was the site of an old burn, and numerous dead logs and stumps littered the area. These provided an ideal habitat for ants and numerous beetle larvae. The area was surrounded by a predominant growth of gray birch (*Betula populifolia*) up to 20 feet high. Oak-sprout growth was the next most abundant woody plant. Scattered white pines (*Pinus strobus*) up to 60 feet high were found at various distances from the perimeter of the field. The ground was exceedingly dry and well drained. Within 100 yards were two old gravel pits which often contained moist or wet bottoms, and these were occasionally visited by the birds. The field was used by at least one singing male each spring. One of the males was captured and banded in April 1955, but was not netted during the summer.

Area 2, South Side of Quabbin Reservoir.—The second area was almost two acres in size and situated near the top of a high hill. Part of it was an abandoned field with low-bush blueberries and scattered white pines. The favorite alighting area was a bare space of about an acre. Several years ago, machines scraped all the topsoil off the site. Vegetation was sparse and the soil rocky. Numerous ant holes were scattered in the area, but the habitat was not nearly as favorable for insect life as Area 1. The fringe of the field on one side was a red pine (*Pinus resinosa*) plantation,

and on the other, low gray birches, poplars (*Populus tremuloides*), and other scattered hardwoods. The border growth on the whole was higher than that on Area 1. There has always been a high breeding population near this area, and six singing males were heard in the vicinity in the spring. All these males were captured and banded in the springs of 1955 and 1957, but none were netted as repeats in the summers.

Area 3, South Side of Quabbin Reservoir.—This was an abandoned field of several acres in extent. It was filled with scattered clumps of high-bush blueberries (*Vaccinium corymbosum*). Being open to the public, there were well-beaten paths around all the blueberry bushes in July. These relatively bare paths at the base of the bushes were the favorite spots sought by woodcocks each evening. The birds flew from neighboring woods and were seen on occasion to come from at least 300 yards away. There was a minimum of eight "singing" males on this area in the spring of 1955. This would have been a difficult field to net, and netting was not attempted because there was little question that nets would be interfered with by the public.

Area 4.—This field was found in 1958 and netted in 1959. Situated on Mt. Pleasant on Prescott Peninsula in Quabbin Reservation, this site was on the highest point of the peninsula, approximately 1,100 feet above sea level. It was surrounded by old abandoned fields planted to Norway spruces (*Picea abies*), red pines, and larches (*Larix laricina*). Gray birch was scattered about on the periphery. Enough open places remained so that the breeding population within a radius of half a mile had not diminished appreciably for ten years. It was an old hayfield of about two acres in size with an adjoining ½-acre field grown up to sweet fern and grassy spots. Birds alighted all over the area, but avoided the heavy, long-grass hummocks.

"Singing" male woodcocks have used this field and adjoining areas for ten years.

POPULATION COMPOSITION OF NETTED SUMMER BIRDS

Composition of birds captured are depicted in Table 1.

Ages of birds captured before the molt were determined by the color on the tips of the scapular and back feathers as described by Duvall (1956). Some young birds caught early in the summer peeped in the net with the same note of newly hatched chicks. August and September birds could not be aged with certainty during night banding. Sex was determined by bill length and width of outer primaries (Greeley, 1953).

Examination of Table 1 suggests that captured birds may not be representative of the actual sex and age ratios existent in the population. The results reveal that the sex and age groups in order of number of captures were juvenile males, adult females, juvenile females, and adult males. These proportions were relatively consistent from one year to the next. Because

TABLE 1

SEX AND AGE RATIOS IN NEAREST WHOLE PERCENTAGES OF 483 WOODCOCKS CAPTURED IN MASSACHUSETTS DURING SUMMERS 1955–1959

Year	Ad. ♂	Juv. ♂	Ad. ♀	Juv. ♀	Tot. Juv.	Tot. Ad.	Total ♂'s	Total ♀s
1955	7(7)*	41(42)	27(28)	25(24)	66(66)	34(35)	49(49)	51(52)
1956	21(28)	32(44)	31(42)	16(22)	49(66)	51(70)	53(72)	47(64)
1957	20(13)	30(19)	36(23)	14(9)	44(28)	56(36)	50(32)	50(32)
1958	14(10)	42(30)	26(19)	18(13)	60(43)	40(29)	55(40)	45(32)
1959	10(11)	35(38)	28(31)	27(30)	38(42)	62(68)	44(49)	56(61)
Totals	14(69)	34(166)	30(143)	20(98)	56(271)	44(212)	50(242)	50(241)

* Figures in parentheses denote numbers of birds.

of this, I doubt that such differences are due to an inadequate sample, but reflect differences in activities of birds according to sex and age.

Reasons for these assumed behavior differences are purely speculative. Adult males may be less active in summer due to a strenuous breeding season extending from late March to early June. Juvenile males may have a greater tendency to move about, a characteristic of many juvenile male vertebrates. Adult females become more active after spending the spring on the ground incubating eggs and rearing young. It is possible evening flights may be serving to develop wing strength for the fall migration.

BEHAVIOR DURING FLIGHTS

Woodcocks were seen flying into the fields one-half hour after sunset at the same light intensity as the beginning of the courtship performance earlier in the year. Usually the flights lasted no longer than 15 minutes, but on one bright moonlight night birds continued to come into one field for 30 minutes. Observations indicate that, after alighting, birds remained in the field from 10 minutes to one-half hour unless flushed. Nets left all night yielded no additional birds.

Birds came in singly as well as in groups of two, three, and four individuals. Figure 1 depicts observations on Netting Area 2 on the evening of 20 June 1959, before netting had started. Twenty-four birds were counted. Only those visible against the evening sky were tabulated. A number of others were heard crossing the field below skyline. Although the figure depicts birds approaching from all points of the compass, the majority came from the western sector and often circled the field and made the final approach from any direction. The pattern of approach depicted was typical of the flights of incoming birds in the other netting areas.

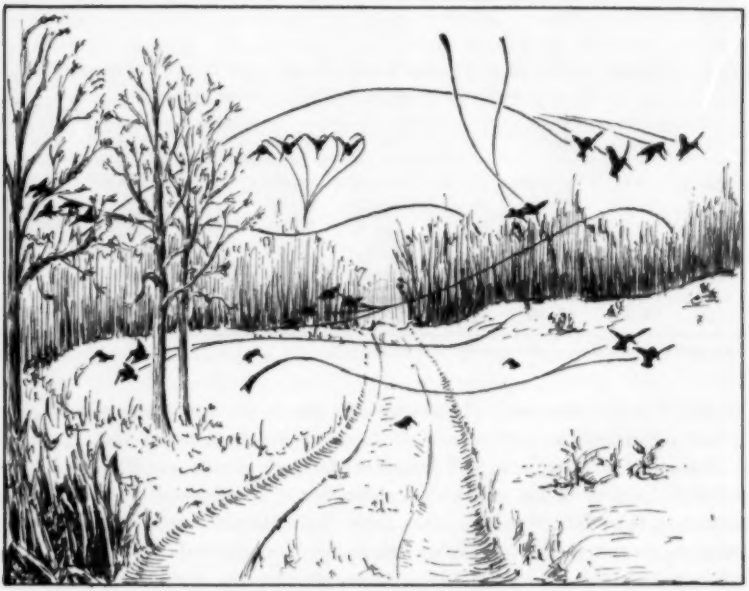

FIG. 1. Woodcock crepuscular flight into open field—Area 2.

Although there is no certain proof, there is no evidence that broods remain intact up to the time the young birds take part in these evening forays. Additional data on this are presented in a later section.

The counts of birds in evening flights when no netting is being conducted may give a rough index of annual abundance if the habitat remains static. Area 1 is in an area of deteriorating woodcock habitat due to vegetative succession. In 1951, there were 63 "singing" grounds known to be occupied in Prescott Peninsula. Censusing the same routes in 1959 indicated only 17 "singing" sites were occupied. Area 2 is on the top of a steeply drained hill which has wet seepages in normal summers. In 1957, the entire hill was dry due to a severe drought. Because of this condition, the birds apparently shifted their diurnal resting areas and used different fields for their crepuscular visits.

From 1952 to 1959 when netting usually took place every evening all summer, records were kept of birds observed and of trap success by weeks and months. It was suspected that the netting and banding operations disrupted normal evening behavior and prompted birds to seek other evening feeding grounds. In 1960, when no nets were set, evening observations of

some of the fields were conducted weekly from late June until the end of the first week in August. The evening flights with some variations continued unabated until nets had to be set to capture some live birds for insecticide studies. After six days of netting on two areas, the nets were removed. From the first night of netting the numbers of birds using the fields fell off steadily. In addition to the 1960 observations the largest number of birds observed in a netting area was on 15 August in a season before netting took place.

Variations in counts on Area 1 before netting were approximately 25–43, on Area 2, 10–27, and Area 4, 20–38. Such high counts over a period of time never were recorded while netting was taking place.

Semi-courtship Activities.—The juvenile male birds approaching the fields early in the summer often performed a "courtship" flight high over the field before landing. The performance closely paralleled the flight of adult males in the spring with the exception that the musical chirp song was not given. Occasional irregular *peent's* were heard on the ground. Most of these males were known to be juveniles, since on some occasions they were captured in nets on their descent. Gonads of collected specimens were minute in size, showing no development. These were not sectioned to discover if there were any active spermatozoa.

On 13 July 1955, Dr. William Nutting of the University of Massachusetts Zoology Department was concealed in small bushes and observed the antics of an apparent male and female on the netting ground a few feet away. From a behavioral point of view, his following description of observations is of interest:

1. Heard *peent* NE at 8:52 and another weak one at 8:54.
2. Several birds in from NNE.

At 8:58, one bird flew in with wing whistle 6½′ from me. He stood and turned SW. Then, I noticed another bird walking in from SW. First bird moved to meet the new one. Bird 1 (hereafter called a *him*) made aggressive head pass toward second (from now on called a *her*). She stopped 2′ from him. He raised his wings, lowered and advanced, raised wings again, lowered and moved; then in several fluttery wing moves came up to female and passed his bill at her midback. She then moved off 3′ NNW. He moved 2½′ NE of her. Both stood still. I heard her give a soft cat wheeze note—followed in a few seconds by another. He turned around and squatted (faced from her). He rose, appeared to peck at ground, then turned facing her. Suddenly he flew in a low arc over her head, wings whistling, to land about 12′ beyond her. She did not change position. In one minute, he flew up with wings whistling and did a semi-courtship flight, directly overhead landing about 50′ to SW. She walked slowly out of sight NW.

I crept toward her and flushed her—her wings fluttered, but didn't whistle. Time, 9:14.

Nutting's description of the behavior of the bird presumed to be a male is similar to the actions of a breeding male preceding copulation. In the course of the Massachusetts studies, hundreds of male birds have been

captured on singing grounds with decoys (Sheldon, 1956*a*, *b*), and many notes were accumulated on the behavior of male birds in the presence of a decoy bird or live female. The latter are invariably approached with raised wings and the copulation act is performed with fluttering wings. Similar observations were made in 1960 on 29 June and 20 September.

The "cat wheeze" note attributed to the female was heard several times on the summer alighting fields. When this note is given, it is often loud and startling, entirely unlike other notes given by woodcocks. Birds flushed from the site of these calls appeared large and were presumably females.

Fall or late summer courtship behavior has been reported on several other bird species including several species of ducks, the Yellow Warbler, Baltimore Oriole, and others (Hochbaum, 1944).

Effects of Weather.—Although it has been pointed out that nets have a deterrent effect on birds, observations of activity in different weather conditions in netting years may well have validity.

Careful weather records kept throughout the years of netting showed slight correlation between weather conditions and bird activity. Windy nights with an air movement of more than 5 mph usually yielded poor catches. The motions of the nets were often detected by the birds and thus avoided. Under windy conditions, few birds usually visited the fields. Clear evenings with temperatures ranging from 55–75°F. often produced good catches, but just as often were unproductive. Still, hot, humid evenings following afternoon thunder showers created conditions which were most consistently productive of birds and often stimulated insect activities. Woodcock activity seemed stimulated by quiet evenings with a light drizzle or fog. On the morning of 16 July 1960 half an hour before sunrise, 64 woodcocks were seen on 3½ miles of road during a light rain. Two mornings later no birds were seen over the same route in clear weather.

Factor of Food.—The most important reason for these flights appeared to be dietary in character. Birds landing in the fields fed actively on various species of insects. Table 2 gives the results of the analysis of stomach contents of 15 birds. Some of these birds were collected as they flew into fields. Although earthworms rank second in percentage of volume, there was little more than a trace in the eight birds which were allowed to feed in the fields 10 or 15 minutes before flushing into the net. Direct observations at dusk include woodcocks actively feeding. One bird alighted on a white rock and was observed picking up food items. Examination of the surface of this rock with the aid of a light revealed numbers of a very small ant. Captive woodcocks have been observed chasing flying insects attracted by a light. Presumably, many birds left damp wooded areas where earthworms were found. Seven birds were collected as they flew into nets before alighting

TABLE 2

STOMACH CONTENTS OF 15 WOODCOCKS NETTED IN FIELDS DURING SUMMER EVENINGS IN MASSACHUSETTS

Item	Family	No. of stomachs	Estimated per cent volume
COLEOPTERA			38.7
Ground beetle larvae	Carabidae	2	
Weevils	Curculionidae	1	
Wireworms	Elateridae	13	
Leaf chafer larvae	Scarabaeidae	1	
Short-winged beetle larvae	Staphylinidae	3	
Darkling beetle larvae	Tenebrionidae	5	
DIPTERA			15.3
March fly larvae	Bibionidae	5	
Long-legged fly larvae	Dolichopidae	4	
	Louchaeidae	1	
Snipe flies	Rhagionidae	8	
Stiletto fly larvae	Therevidae	6	
Root-feeding fly larvae	Tipulidae	1	
LEPIDOPTERA			14.7
Noctuid moth caterpillar	Noctuidae	8	
Pupa		1	
Loopers	Geometridae	1	
ANNELIDA			
Earthworms		8	30.0
CHILOPODA			
Centipede		2	.3
CHELICERAE			
Spiders		2	.3
HYMENOPTERA			
Ants		2	.3
VEGETABLE MATTER		6	.2

in the fields. These contained earthworm remains in their stomachs. It may well be that the high protein content of the insects consumed in the fields formed an important part of the summer diet. English workers on icterid species have observed that seeds or fruits eaten during the molting period have a high protein content.

Although the fields were dry and no probing could take place, the prehensile tip of the woodcock bill is well adapted for picking up insects from the ground or even catching a few in the air.

It will be seen from Table 2 that a large variety of fly and beetle larvae were readily consumed. Analysis of these stomachs suggests that woodcocks often consumed earthworms in their diurnal coverts but visited the fields primarily for other types of animal food.

Summer Evening Activity by Months.—The only valid observations on the activity of birds by months are those observations made when no netting or banding was taking place. Most of these observations were made in 1960. Woodcocks alight in these fields in large numbers as late as mid-August at least. Almost as many can be seen in September but fewer alight in the fields. Birds have been netted as late as 10 October and as early as 13 June. When the fields were netted, no birds were observed on several occasions on all areas during August due to the disturbance of banding.

Evidence that Flights Comprise Resident Birds.—The question is posed as to whether the flights were local movements by different groups of birds each evening. In Netting Area 2, 20 per cent of the captures in 1956 and 1958 were repeats. This was solid evidence that many of the same birds took part in the activity more than one evening. The chances of capturing repeats were small, partly since it was seldom that more than 30 per cent of the birds observed each evening were netted and perhaps, more importantly, because of the deterrent effects of the netting and banding activities referred to in an earlier paragraph. Birds in Netting Area 2 came from a relatively concentrated woodcock range. In contrast, Netting Area 1, which has yielded about 400 of all birds captured, produced few repeats. Birds from this area were surrounded by hundreds of acres of woodcock range, and several have been taken as returns several miles away. This field is small, and many other alighting areas must exist. Limited data on returns described in a later paragraph further suggest that we were dealing with resident birds.

Distance between Alighting Fields and Diurnal Cover.—The actual distance individual birds flew in the evening to reach the netting fields is somewhat conjectural. In Netting Area 1, observers posted at intervals provided evidence that many birds coming into the field were first observed coming east over a large hill half a mile from the landing field. In Area 2, observers have recorded many birds travelling toward the field from distances up to at least ⅓ of a mile. There was no single observation of a bird rising from diurnal cover and flying to the field. It probably took a woodcock no longer than two minutes to fly a mile, and there was no way of knowing how far the birds had come when first observed. In one instance, two juvenile males were captured in a funnel trap on the edge of a large alder swamp two miles from the netting field and separated from it by a large hill. Ten days after the first capture, these two birds were again netted, but there was no method of ascertaining their whereabouts between the two capture dates.

TABLE 3

RETURNS OF WOODCOCKS NETTED IN CENTRAL MASSACHUSETTS DURING SUMMERS 1952–1959

Band no.	Sex	Age when captured	Distance between capture sites in miles	Time lapse between capture sites to nearest year	Method of recapture
553-50260	♀	Juv.	10	2 years	Netted
563-33238	♀	Juv.	0	2 years	Netted
553-50272	♀	Juv.	0	3 years	Netted
563-33297	♀	Juv.	0	1 year	Netted
553-50220	♀	Ad.	3	4 years	Netted
563-33054	♀	Ad.	0	3 years	Netted
563-33110	♀	Ad.	2½	4 years	Netted
563-33160	♀	Ad.	0	2 years	Netted
603-44212	♀	Ad.	0	1 year	Netted
553-50286	♀	Ad.	0	2 years	Netted
523-05229	♀	Ad.	1	1 year	Netted
563-33054	♀	Ad.	0	2 years	Netted
553-50274	♀	Ad.	0	3 years	Netted
563-33295	♀	Ad.	0	1 year	Netted
563-33244	♀	Ad.	0	1 year	Netted
563-33022	♀	Ad.	0	1 year	Netted
563-33242	♂	Juv.	½	1 year	Singing-ground trap
553-50222	♂	Juv.	3	3 years	Netted
563-33213	♂	Juv.	0	3 years	Singing-ground trap
603-44205	♂	Juv.	0	1 year	Netted
603-44225	♂	Juv.	0	1 year	Netted
563-33219	♂	Ad.	⅛	3 years	Singing-ground trap
553-50211	♂	Ad.	1½	1 year	Singing-ground trap
523-07219	♂	Ad.	1	1 year	Singing-ground trap
553-50160	♂	Ad.	1	2 years	Netted
50-301755	♂	Ad.	2	5 years	Netted
563-33266	♂	Ad.	½	1 year	Singing-ground trap
563-33010	♂	Ad.	10	1 year	Singing-ground trap
563-33222	♂	Ad.	1/10	1 year	Singing-ground trap
553-50204	♂	Ad.	0	2 years	Netted
563-33773	♂	Ad.	1	3 mos.	Netted
523-50238	♂	Ad.	1	1 year	Singing-ground trap
553-50162	♂	Ad.	¾	4 mos.	Netted
553-50135	♂	Ad.	1	4 mos.	Netted
563-33243	♂	Juv.	¼	1 year	Singing-ground trap

RETURNS AND RECOVERIES

In this paper, *return* refers to a bird recaptured after a period of at least three months. *Recovery* refers to a bird shot or recovered in a location removed from the study areas. Homing and returns of adult males caught in

the spring on their singing grounds were reported earlier (Sheldon, 1956*a*). Table 3 presents the total data on returns of netted birds.

Returns.—Data from Table 3 offer further evidence that netted birds comprised a resident population. There are more return records on adult males than juveniles, because spring singing-ground trapping activities presented greater opportunity for collecting male return records. These data simply suggested the extent of spring and summer range of some of the netted birds. There was one case of a male and another of a female banded one year in Area 1, and captured as a return in Area 2, a distance of 10 miles.

Although the record is meager, these results suggest homing behavior on the part of all age and sex groups. These data show minimum distances from the netting fields that some individual, netted, resident birds have moved at some time in their lives during spring or summer. Not shown in the table is the instance referred to in a previous section of the netting of two juvenile males two miles from an alder swamp where they had been captured ten days previously in a funnel trap. Far more adequate data presented earlier on adult males (Sheldon, 1956*a*) indicate adult males return in subsequent years to the general vicinity of the breeding grounds where first captured.

This table contributes other incidental information. There is evidence that both sexes breed in their first year. Number 50-301755 was first banded as an adult male at least a year old on a singing ground in April of 1951, and subsequently netted five years later in the summer of 1956. Six years longevity appears to be the longest life span recorded for the American Woodcock in the wild.

Recoveries.—Seventeen hunter-recoveries of birds netted and banded during this study were all from southern migration lanes with the exception of two. One juvenile female banded on 16 July 1956, was shot on 1 October 1957, in Peru, Vermont, 65 miles northwest of the original banding location. This bird conceivably could have been a resident of Massachusetts and exhibited a case of vagrant migration. There seems little question that the second bird had forsaken her rearing grounds. This was another female of uncertain age banded on 1 September 1956, and shot 10 October 1957, in Belfast, Maine, 350 miles northeast of the banding location.

WEIGHTS

Weights of known juveniles and adults have varied little from year to year. Figure 2 shows the overlap in weight of the different age and sex groups. By the time juveniles were active enough to take part in evening flights, weight was an unsatisfactory criterion for separating the age groups. Table 4 represents weight changes in three adults and 12 juveniles captured twice at intervals of at least ten days. Weight changes of a few grams are of no significance.

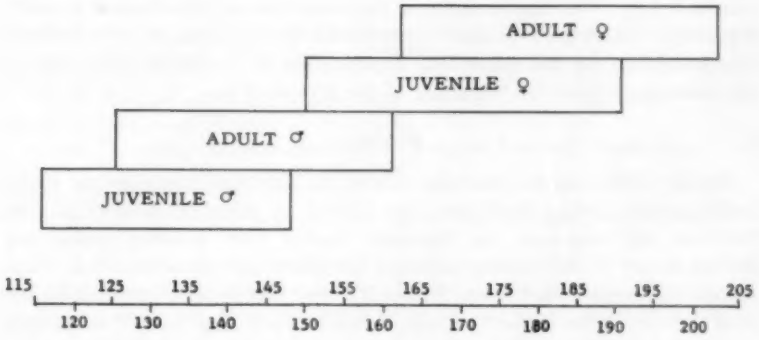

FIG. 2. Weights in grams of 112 woodcocks netted in Massachusetts in the summer of 1956.

Subsequent weighing of a large number of captive birds demonstrated weight fluctuations depending on when the birds had last consumed a meal. Each bird ate approximately 150 grams of earthworms every 24 hours. Because of rapid metabolism and digestion, weights would seldom vary more than 20 or 30 grams. Table 4 offers evidence that juveniles had attained mature growth by the time they engaged in evening flights. If growth had not ceased, much greater changes in weight would have taken place. The greatest gain took place with one adult female and two juvenile females first

TABLE 4

CHANGES IN SUMMER WEIGHT (IN GRAMS) OF 15 WOODCOCK CAPTURED TWICE AT INTERVALS OF AT LEAST 10 DAYS

Sex	Age	Date first caught	Weight when first caught	Date of second capture	Weight on recapture	Weight change
♂	Ad.	25 June '57	127	18 July '57	132	+ 5
♂	Juv.	13 June '57	126	25 June '57	129	+ 3
♂	Juv.	25 June '57	147	12 July '57	150	+ 3
♂	Juv.	23 June '57	121	23 July '57	124	+ 3
♂	Juv.	6 July '56	139	30 July '56	142	+ 3
♂	Juv.	25 June '58	158	23 July '58	155	- 3
♂	Juv.	29 June '58	135	23 July '58	145	+ 10
♀	Ad.	3 July '56	165	28 Aug. '56	184	+ 19
♀	Ad.	30 June '58	165	20 July '58	170	+ 5
♀	Juv.	19 June '57	154	7 July '57	171	+ 17
♀	Juv.	26 June '57	173	12 July '57	187	+ 14
♀	Juv.	13 June '57	184	1 July '57	184	0

caught 3 July 1956, and recaptured the same year in late August or early September. These gains probably represented the beginning of fat accumulation preceding the fall migration. Examination of specimens taken late in the summer revealed the beginning of the growth of fat.

MOLTING

Duvall (1956) has described methods of distinguishing juveniles and adults in the summer, before the former have molted, by plumage characteristics on the back and scapulars. An important finding from summer netting has been a record of the molting sequence for adults and juveniles. This information will be published later. Suffice it to say that because juveniles do not molt their primaries in the first year, a careful study of primary feather wear revealed a method of aging fall-shot woodcocks by examination of one wing (Sheldon, Greeley, and Kupa, 1958). To further apply this technique, large fall wing-samples have been collected from hunters in the northern breeding grounds. Data gathered from this source should greatly augment our knowledge of annual population and production trends. Greeley (1953) has described a method of sexing woodcocks on the basis of outer primary width; so sex as well as age ratios can be calculated from wing collections.

SUMMARY

Seven hundred and forty-six woodcocks captured by Japanese mist nets at dusk in fields provided significant data on summer behavior of this species. The alighting areas varied in size and vegetative composition, but all were situated near the center of spring breeding grounds. The sex and age composition of birds captured showed a preponderance of juvenile males and adult females. Reasons for such age and sex discrepancy are discussed. Factors prompting these evening flights are suggested. Evidence points to food as the most important factor. Behavior of these birds has been described. The alighting grounds were dry and the food consisted primarily of fly, beetle, and moth larvae. Returns suggest homing behavior on the part of all age and sex groups. Molting studies of these summer birds provided the technique for aging and sexing wings of fall-shot birds.

ACKNOWLEDGMENTS

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ENERGY OF BIRDS CONSERVED BY ROOSTING IN CAVITIES

S. Charles Kendeigh

Nighttime is a critical period in the resistance of birds to winter cold at high latitudes because this is generally the coldest time of the day, and is a period when diurnal birds are unable to feed. Numerous notes in the literature describe how birds seek dense vegetation or cavities of various sorts for roosting purposes (Frazier and Nolan, 1959). Shelter obviously gives them protection from the wind and decreases the rate of heat lost from their bodies, but quantitative measurement of the benefits thus obtained has rarely been obtained (Gerstell, 1942).

The present study was stimulated by observing a House Sparrow (*Passer domesticus*) going night after night into a bird nesting box attached to the side of the Vivarium Building on the University of Illinois campus. An attempt was made to determine the difference between the temperature inside the box while the bird was roosting in it at night and the temperature immediately outside the box.

Observations on the roosting of the House Sparrow have been reported by Labitte (1937), Dunsheath and Doncaster (1941), and Swaine (1945), among others. Dunsheath and Doncaster many times observed apparently paired birds roosting together. Swaine reports that the House Sparrow often roosts in its own nests during the winter. He usually found only one bird in a nest at a time, but on four occasions found pairs of birds using the same nest, and on one occasion three birds. I never suspected more than one bird to be using the box in this study, but at different times observed a male and a female at the box at roosting time.

The box was made of ¾-inch pine lumber. Inside dimensions were 6 inches front to back, 4 inches side to side, and 5 inches top to bottom. There was a flat top hinged on one side. An entrance-way with a diameter of 1½ inches was located in the front, ½ inch below the top, and the entire front could be tipped open on a pivot near the top. The box was on the south side of the building approximately 40 feet from the ground. Since it was placed under the rather wide eaves of the roof, it was well protected from precipitation. The box-cavity was about one-half filled with old nesting material, and the nest-cavity, in the rear half of the nesting material, was lined thickly with chicken feathers. The bird presumably roosted in the nest-cavity, but this was not verified.

PROCEDURE

Two thin insulated copper-constantan thermocouples were prepared and when tested against a standardized mercury thermometer gave identical aver-

age readings at 22.9° and –13.4°C and a standard deviation for 24 individual readings of ± 0.15°C. One thermocouple was fastened inside the box directly over the nest-cavity with the sensitive junction projecting slightly so as to record the air and not the wall temperature. There was no suspicion that the thermocouple was in a heat stream. The other thermocouple was fastened to the middle of the east side of the box on the outside with the junction projecting into the air. This junction was protected from direct solar radiation at all times of the day.

The two thermocouples at the box were connected to thick copper and constantan leads that extended 200 feet to a Leeds and Northrup recording potentiometer inside the building. The potentiometer registered over a range of –40° to + 160°C with the chart graduated in 2°C intervals. Temperature recordings were interpolated to 0.5°C for analysis. Experience with this potentiometer has shown that while individual readings could be in error by ± 1.0°C, averages were dependable within ± 0.5°C. A daily check on the accuracy of the recording was obtained by the outside and inside thermocouples registering identical temperatures while the bird was absent during the daylight hours. The three thermocouple outlets of this potentiometer were interconnected so that two consecutive readings were taken of the inside box temperature, then one of the outside temperature, each at one-minute intervals, with this cycle being repeated continuously.

RESULTS

Complete 24-hour per day recordings were obtained for 23 days, beginning 20 December 1949, and ending 11 January 1950. The bird entered its roost, on the average, a few minutes after 4:00 PM and left it a few minutes after 7:00 AM, CST. This gave a roosting period of 15 hours per day. On 1 January, the sun sets at 4:38 PM and rises at 7:15 AM.

When the bird first entered the box, inside box temperatures registered higher for a period of one-half to one hour than during most of the night, presumably due to restlessness of the bird (Fig. 1). The temperature record indicates that thereafter the bird was quiet for periods up to two hours or longer during which the box temperature remained uniform. These quiet periods were terminated by short abrupt rises in box temperature, occasionally amounting to over 3°C. These temporary rises in temperature are unexplained, but must have resulted from some activity of the bird. As the outside air temperature fell during the night, the difference between the temperatures inside and outside the box regularly became greater. For one-half to one hour before the bird left in the morning, restlessness, apparently, again brought a higher box temperature, similar to that in the evening after the bird entered. After the bird left the box, the box temperature fell rapidly, but required up to 45 minutes to reach the outside air temperature.

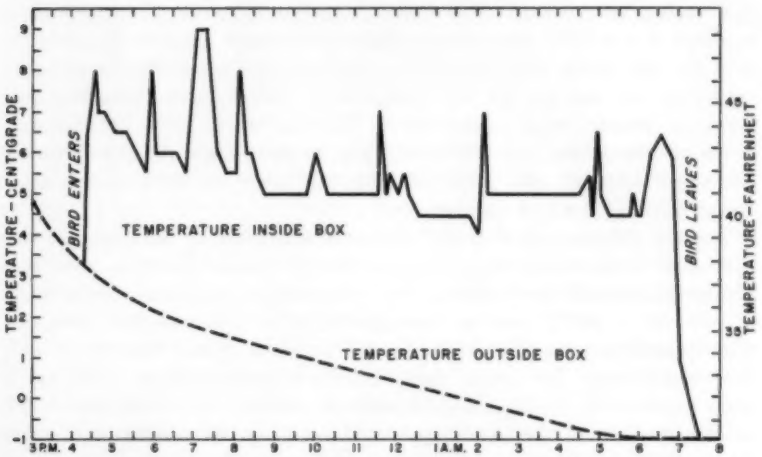
TEMPERATURE - CENTIGRADE
TEMPERATURE - FAHRENHEIT
BIRD ENTERS
BIRD LEAVES
TEMPERATURE INSIDE BOX
TEMPERATURE OUTSIDE BOX
3 PM. 4 5 6 7 8 9 10 11 12 1 A.M. 2 3 4 5 6 7 8

FIG. 1. Temperatures inside and outside the box on a representative night, 10–11 January 1950.

The night of 21–22 December 1949, was unusual in that air temperatures dropped from around 11°C a little before 11:00 PM to −3°C at 8:00 AM, this drop being accompanied by rain (Fig. 2). Inside box temperatures fell from about 13.5°C to + 3°C. Here again it is evident that the difference between the temperatures inside and outside the box was less at the higher than at the lower temperatures.

It is obvious from Fig. 2, but not from Fig. 1, that a pronounced change in the outside air temperature will bring a change in the inside box temperature. In order to show the relation between inside box and outside air temperatures the nightly mean of each of the two temperatures was obtained for each of the 23 days. The means were computed only for the hours 6:00 PM to 6:00 AM, inclusive, in order to avoid the restless periods of the bird after entering and before leaving the box each night. One temperature was read from the chart for each hour on the hour, an average value being recorded if the temperature was fluctuating at the time.

When the differences between the two temperatures are plotted against the temperatures outside the box (Fig. 3), a linear relation is evident ($b = -0.19$°C; $P = < .001$). The same regression line is obtained by plotting the differences between the hourly temperatures rather than the differences between the mean nightly temperatures. The lower the outside air temperature, the greater the difference between outside and inside box

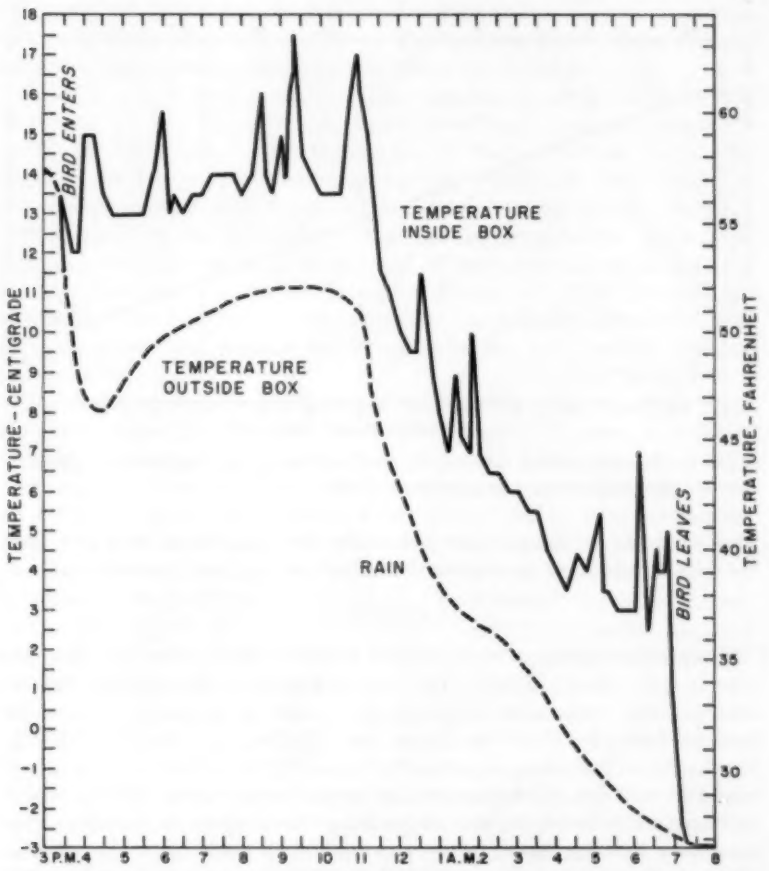
BIRD ENTERS
TEMPERATURE INSIDE BOX
TEMPERATURE OUTSIDE BOX
RAIN
BIRD LEAVES
TEMPERATURE - CENTIGRADE
TEMPERATURE - FAHRENHEIT
3 P.M. 4 5 6 7 8 9 10 11 12 1 A.M. 2 3 4 5 6 7 8

FIG. 2. Temperatures inside and outside the box on an unusual night, 21–22 December 1949.

temperatures, although the increase in the difference does not equal the drop in the air temperature, for instance:

Outside air temperature	+17°C	−8°C
Difference	1.5	6.2
Inside box temperature	18.5	−1.8

An extension of the line in the upward direction indicates that the bird would not raise the box temperature at air temperatures of 24.7°C and above. At these higher air temperatures, the resting metabolism of the

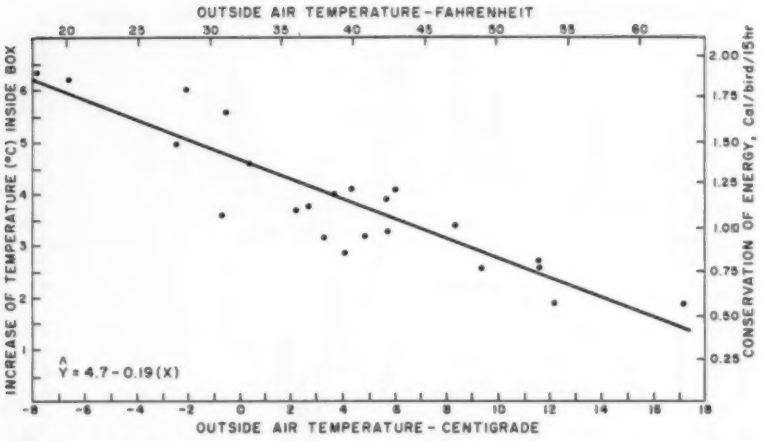

FIG. 3. Relation between box temperatures and outside air temperatures correlated with the amount of energy conserved by the bird.

bird would be so reduced that apparently the low rate of heat loss from the bird would have no measurable effect on the box temperature.

DISCUSSION

Temperature relations inside a well-insulated cavity, like this box, are complicated (Moore, 1945). The resting bird at night probably has an internal body temperature of about 40°C. Skin temperatures beneath the feathers would be about one degree less (Baldwin and Kendeigh, 1932). Conduction of heat along or across the feathers to the outside of the plumage would be very slow, so the temperature on the surface of the plumage would be considerably below the skin temperature. Roosting birds in cold weather commonly fluff out their feathers and place their heads under the scapular feathers. This increase in the thickness of the plumage greatly reduces the rate of heat conduction away from the body. The low surface temperature would greatly diminish the amount of heat radiation from the bird to the walls of the box. Heat conduction from the body and legs of the bird to the nest-material in the box would be very small. Likewise, evaporation of moisture in the respiratory system would account for only a small loss of heat. The principal pathway of heat loss from the bird would doubtless be convectional, partly by the air being warmed by the heat conducted to the surface of the plumage, but to a greater extent by the expiration of heated air from the body in each breathing cycle. This would warm the box cavity until a temperature was reached where the loss of heat from

the box to the air balanced the heat loss from the bird to the box. Radiation of heat from the box to the sky during clear weather was doubtless reduced because of the position of the box under the eaves of the roof.

Wood is a poor heat conductor. The temperatures of the inside surface of the walls of the box, although not measured, may have approached the inside air temperature. The temperature of the outside surface of the walls of the box probably approximated the outside air temperature. A temperature gradient must therefore have occurred in the ¾-inch wall, equal approximately to the difference in box and air temperature. Heated air rises and there was doubtless an exchange of warm for cold air through the small entrance-way and the crack between the top lid of the box and the side walls. The insulation of this roost-site was probably better than that of most species but perhaps not as good as for some, as for instance woodpeckers.

The resting or standard metabolism of the House Sparrow at night is lower than it is during the daytime. Seven measurements obtained at night at constant temperatures from −19°C to + 31°C (Kendeigh, 1944) indicate a straight-line relation between resting metabolism and temperature ($b = -0.699$ small calories per gram per hour; $P = < .001$). If we assume the mean weight of House Sparrows in December and January to be 28.5 grams and the roosting period per day to be 15 hours, then for each rise of 1°C in inside box temperature there would be a daily conservation of 0.30 large calories of energy to the bird. These caloric values have been incorporated in Fig. 3. The resting metabolism of the bird in large calories ($\hat{Y}$), when X is temperature, follows the equations:

$$\hat{Y} = \frac{25.6 - 0.699(X - 11.3) \times 28.5 \times 15}{1000} \text{ or } \hat{Y} = 3.4 - 0.299X$$

At + 17°C, the raising of the roosting temperature by 1.5°C would conserve 0.45 kcal or only 4.9 per cent of the total required by the resting bird. At −8°C, however, the difference of 6.2°C would mean a saving of 1.86 kcal or 11.1 per cent. Were nightly temperatures to drop to −20°C, an extension of the curvilinear line (Fig. 4) indicates that 12.6 per cent of the total energy required for roosting would be conserved, at −30°C the saving would be 13.4 per cent. The species regularly experiences air temperatures as low as these. An extension of the line in the other direction indicates that no energy would be saved at 24.7°C.

It would certainly appear that roosting in cavities has an advantage at low temperature which increases in extent, but not directly proportionally, with the drop in air temperature. The amount of energy thus conserved may make the difference between survival and death during periods of extreme weather during the winter. Likewise, roosting in cavities may enable a

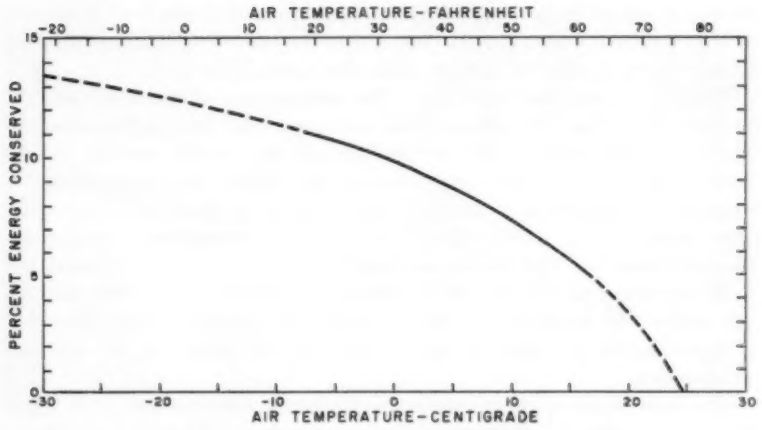

FIG. 4. Relation between per cent of energy conserved by roosting in cavities and air temperature.

species to occur farther north during the winter than it otherwise would. Further studies along these lines should be made with refined techniques.

CONCLUSIONS

1. The temperature inside a box cavity used for overnight roosting by a House Sparrow was higher than the outside air temperature at air temperatures below 24.7°C ($\hat{Y} = 4.7 - 0.19\ X$).

2. The difference between temperatures inside and outside the box cavity increased with a drop in temperature ($b = -0.19$°C).

3. The energy conserved by roosting in a cavity compared with roosting in the open varies curvilinearly from zero at + 24.7°C to 13.4 per cent at −30°C.

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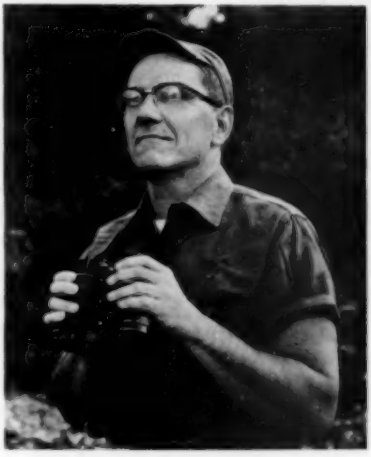
NEW LIFE MEMBER

George A. Hall, holder of a Ph.D. from Ohio State University and now Associate Professor of Chemistry at his baccalaureate Alma Mater, West Virginia University, Morgantown, West Virginia, is seriously interested in ornithology and has contributed to the literature of the field. His chief interests are in breeding bird populations, and in geographical and ecological distribution of birds. He has served as a regional editor for *Aududon Field Notes*, and has contributed numerous notes in *The Redstart* and several population studies in *Audubon Field Notes*. Dr. Hall served the Brooks Bird Club as president from 1952 to 1955, and is currently the editor of their journal, *The Redstart*. He is a member of the AOU, the Cooper Ornithological Society, and the Wisconsin Society for Ornithology.



A BOTANICAL ANALYSIS OF KIRTLAND'S WARBLER NESTS

WILLIAM E. SOUTHERN

THE Kirtland's Warbler (*Dendroica kirtlandii*) is of special interest to ornithologists because its breeding range is restricted to the distinctive jack-pine (*Pinus banksiana*) plains of the northern part of the Lower Peninsula of Michigan. The 1951 census of this species reported by Mayfield (1953. *Auk*, 70:17–20) indicated that the total population at that time was about 1,000 individuals. The species is most common in four (Crawford, Oscoda, Iosco, and Montmorency) of the 12 counties where nests have been recorded. The breeding range of the species is less than 85 by 100 miles in size. A portion of the data accumulated during this study appeared in H. Mayfield's book, "The Kirtland's Warbler" (1960. Cranbrook Institute of Science). Data so used are indicated in this paper.

Ornithologists have been puzzled by the restriction of the Kirtland's Warbler to a portion of Michigan's jack-pine regions. Mayfield (op. cit.) suggested three interrelated factors as an answer: (1) porous soils, (2) suitable ground cover, and (3) large tracts of young jack pines. In this study I attempted to determine whether or not the materials used in the warbler's nests, since they are obtained from the ground cover, aided in restricting the species to the more open pine forest.

According to Zimmerman (MS) the jack-pine plains may be divided into three parts: (1) the forest—large, fairly dense stands of jack pine; (2) savannas—stands of open, scattered jack pines, and sometimes a few other species; (3) burns—regions in which the stands of large trees have been destroyed and natural reforestation is taking place. The Kirtland's Warbler nests only in savannas and burns. Therefore, only the vegetation of these formations is considered here.

In this study I examined 25 Kirtland's Warbler nests. Twenty of these nests were taken apart and the materials identified, when possible, and weighed. Measurements were recorded; only the 16 nests that contained eggs were used in computing average dimensions since nests that contained young were probably stretched out of shape. During the summer of 1958, I made a botanical study of a section of Kirtland's Warbler habitat in Presque Isle County. Some of the data from that study are included in this paper.

I wish to express my appreciation to Dr. Elzada Clover, Dr. Charles Conrad, Mr. Mason Fenwick, and to Dr. Edward Voss for their assistance in the identification of plant materials. Dr. Voss also made available the University of Michigan Herbarium for comparison of specimens. All of the nests used in this study were from the collections of the University of Michigan Museum of Zoology. Dr. Dale Zimmerman and Mr. Harold Mayfield made available their manuscripts and permitted me to use pertinent information. Dr. Harrison Tordoff made valuable suggestions during the preparation of the manuscript.

The flora of the pine plains is made up of approximately 175 species of higher plants and some 15 species of lichens, mosses, and ferns. In few parts of the dry, sandy, upland pine plains are there luxuriant growths of vegetation. The coverage is much greater in some regions but it is often possible to find sand showing through the ground cover; in some localities fairly large expanses of sand supporting little besides mosses are evident.

The jack pine is the dominant tree of the pine plains but numerous oaks (*Quercus*), occasional aspens (*Populus*), some cherry (*Prunus*), and a few red pines (*Pinus resinosa*) may be interspersed. Red pine plantations are found in some localities. If deciduous trees become too numerous the warblers no longer use the habitat.

The Kirtland's Warbler appears to require an open stand of pines which allows filtered light penetration. This is best offered by stands of jack pines 6 to 15 feet high. Dense "islands" of pines usually exist with openings of herbaceous plants between. Mayfield (op. cit.) stated that the penetration of sunlight increases the life span of the lower branches and thus provides cover nearer the ground and nest. The nest of the warblers may be located on the ground within or at the edge of such an "island." The nests examined were constructed in depressions that ranged from 29 to 41 mm deep in the duff.

All of the nests used in this study were collected in Crawford and Oscoda counties. The vegetation and soil surrounding some of the nests were also collected. These samples indicated that no specific type of vegetation, other than a sizable clump of grass or small shrubs, was consistently used for concealment of the nest. Vegetation was completely arched over some nests thus permitting entrance from only one side.

The average dimensions of the Kirtland's Warbler nests were as follows: Outside diameter, 104 mm by 96 mm; inside diameter, 61 by 56 mm; outside depth, 48 mm; inside depth, 34 mm. The average thickness of the walls was 40 mm, and that of the nest bottom 14 mm. The rim was often asymmetrical and sometimes as much as 15 mm thicker than the rest of the nest wall (Fig. 1). The average weights of the dried nests was 13 grams. The construction varied as to its sturdiness. Some nests were loosely made, others tightly so. A few nests had thin places in the sides through which light passed (see Mayfield, pp. 74 and 75).

There were three recognizable layers in most of the nests (Fig. 1): (1) A loose outer layer made up of coarse stems, leaves, and rootlets of *Carex pensylvanica*, some grasses, leaves, pine needles, and a few short sticks; (2) a middle layer of more tightly woven finer grasses; and (3) the inner layer or lining that was usually of deer hair, mosses, fine twigs, or an unidentified black fiber.

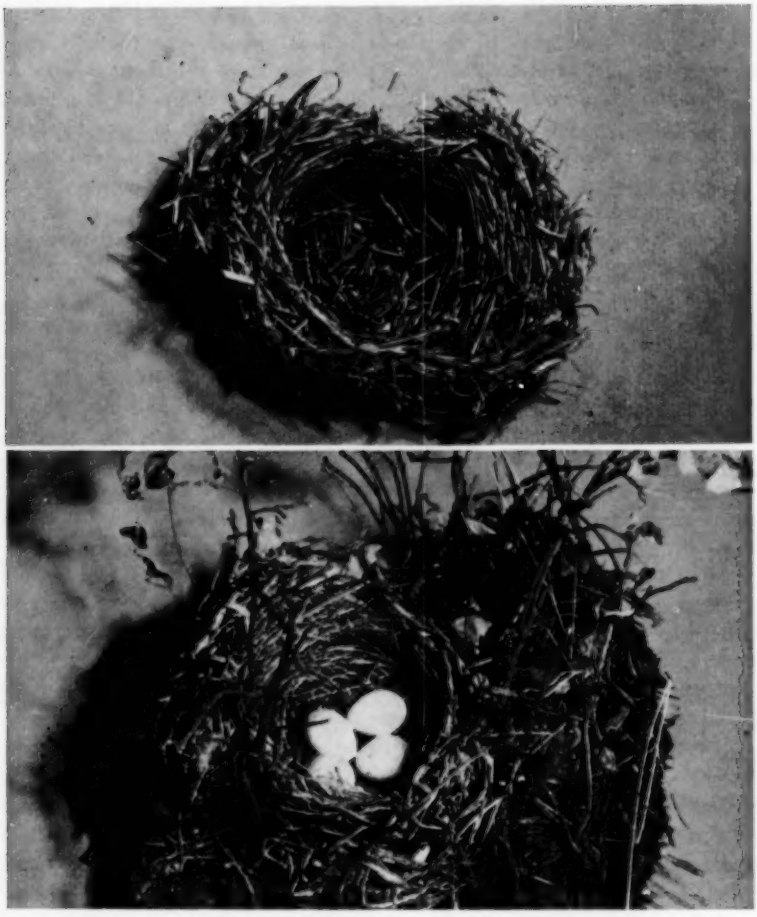


FIG. 1. Rims of nests were asymmetrical, thickened, and composed of coarser material.

At least 29 species of plants were used in the nests. Most of the species used were fairly common within the burns or savannas but none was peculiar to the pine plains.

I placed the materials found in the nests into 11 categories listed below; under each category are the species of plants included, part of the plant used, range of amounts used per nest, average lengths of the pieces, and the percentage of nests containing each type of material. The relative abun-

dance in the region (Zimmerman MS) of each species of plant used by the warblers is also given. A table summarizing the following data appeared in Mayfield's monograph (op. cit.).

COARSE GRASSES AND SEDGES.—These materials were the bulk of the outside layer of all nests. Amounts ranged from 60 to 97 per cent (av. 56.34 per cent) of the total weight of the nests. Lengths of five leaves selected at random from each of 10 nests ranged from 72 to 170 mm (av. 124 mm). The average width of the pieces was 1.6 mm.

Carex pensylvanica.—Present in 12 nests; the basal tufts were commonly used and perhaps many leaves were present, but positive identification was impossible. Zimmerman gave the constancy (percentage of times found in his quadrats) for burns as 100 per cent, and savannas 94 per cent.

Agropyron sp.—Leaves and stems of this grass were used in at least four nests. It is apparently rare within the pine plains but may be fairly common along roadsides.

Sorghastrum sp.—Leaves and stems present in one nest. Constancy 20 per cent in savannas, 9 per cent in burns. According to Zimmerman, *Sorghastrum* occurs very rarely in forest openings and not at all in shaded woodlands.

Agrostis scabra.—Leaves, stems, and some fruiting bodies used in one nest. Constancy in burns 27.2 per cent, savannas 7.9 per cent.

Eragrostis spectabilis.—Leaves were used in two nests. This grass provided surrounding cover for at least one nest. Zimmerman does not list it for the pine plains.

Andropogon sp.—Leaves and stems used in two nests. Zimmerman found two species on the pine plains, *A. gerardi* and *A. scoparius*. Respectively, their constancies are, burns 54 per cent, interior savannas 50 per cent, peripheral savannas 16.6 per cent; burns 90.9 per cent, and savannas 94.0 per cent.

FINE GRASSES.—These were the major constituents of the middle layer and, to a lesser extent, the lining of 22 (88 per cent) of the nests. Amounts ranged from a trace to 30 per cent (av. 9.85 per cent) of the total weight of a nest. Fruiting bodies, leaves, and stems were used. Lengths of the stems used ranged from 94 to 178 mm (av. 141 mm).

Deschampsia flexuosa.—Found in five nests. Constancy in burns 27.2 per cent, savannas 18.0 per cent.

Muhlenbergia glomerata.—Identified from three nests. Considered to be rare in the pine plains. Zimmerman collected it in a single Oscoda County savanna.

Agrostis scabra.—Used in middle layer and lining of 11 nests as well as in outer layers as mentioned previously.

Danthonia spicata.—Present in three nests. Constancy 63.6 per cent in burns, 82.0 per cent in savannas.

Poa compressa.—Occurred in five nests. Constancy in burns 63.6 per cent, savannas 32 per cent. Zimmerman also listed *P. pratensis* for one small area of the pine plains.

Oryzopsis asperifolia and *O. pungens.*—One or the other occurred in five nests. The first is considered generally rare by Zimmerman. The latter is much more common; constancy 54.5 per cent in burns and 16 per cent in savannas.

Festuca saximontana.—Identified from three nests. Constancy 9 to 10 per cent in burns and savannas. *F. scabrella* was also listed by Zimmerman and has a very similar constancy. However, it seems to be limited to more open areas. There is still the possibility of confusion of specimen material.

PINE NEEDLES.—Needles were found in every nest examined. Although needles were scattered through parts of all layers of some nests, the greatest percentage was usually in the outside layer.

Pinus banksiana.—Needles occurred in 25 (100 per cent) of the nests. Amounts ranged from 0.1 to 9.0 (av. 2.22) per cent of the total weight. Needles were found in all parts of the nests but were most abundant in the outer layer.

Pinus resinosa.—Needles occurred in 5 (20 per cent) of the nests. The amounts ranged from a trace to 1.5 per cent (av. 0.41) of the total weight. The needles were scattered through the outer portions of the nests but never occurred in the middle layer or lining. This species of pine occurred in 14.3 per cent of Zimmerman's quadrats. Zimmerman studied one nest of the Kirtland's Warbler from a stand of *P. resinosa* and found that needles of this species made up 30 per cent of the outer layer of the nest.

Mosses.—The reddish-brown sporophytes of *Polytrichum piliferum* occurred in the linings of 22 (88 per cent) of the nests studied. Vegetative portions were occasionally found in other layers of the nest. Amounts ranged from a trace to 8.5 per cent (av. 2.55 per cent) of the total weight of the nests.

Twigs.—Fine brownish stems of *Polygonella articulata* are included under this category. *Polygonella* occurred in 9 (36 per cent) of the nest linings. Amounts ranged from 0.8 to 9.9 (av. 1.8 per cent) of the total weight. On no occasion were both *Polytrichum* and *Polygonella* present in a nest lining. Constancy of *Polygonella* was 9 per cent in burns and 14 per cent in open savannas. It was more common along roadsides. Stem lengths ranged from 56 to 61 mm (av. 58 mm).

Coarser twigs were found in outer portions of 18 (72 per cent) of the nests. Pieces were usually short and dark in color. Diameters ranged to 4 mm. Amounts per nest ranged from 0.1 to 5.7 (av. 1.55) per cent of the total weight. The following woody plants were represented: *Quercus* spp., *Pinus banksiana*, and *Vaccinium angustifolium*. Lengths ranged from 16 to 52 mm (av. 33 mm).

Leaves.—Leaves of deciduous trees, shrubs, and herbaceous plants occurred in 20 (80 per cent) of the nests. Amounts ranged from a trace to 4.3 (av. 1.27) per cent of the total weight. Small leaves or portions of larger ones were used. Plants represented were *Quercus* spp., *Salix* sp., *Vaccinium angustifolium*, *Comptonia peregrina*, *Prunus* sp., *Arctostaphylos uva-ursi*, and *Epigaea repens*.

Rootlets.—Relatively unimportant amounts of small rootlets were found in 9 (36 per cent) of the nests. Amounts ranged from a trace to 2.25 (av. 0.41) per cent. Rootlets were present in nest linings. Generally only one or two pieces, if any, were found per nest.

Lichens.—Small amounts of *Cladonia* spp. ranging from a trace to 1.5 (av. 0.55) per cent occurred in 9 (36 per cent) of the nests studied.

Black fibers.—Fibers occurred in 8 (32 per cent) of the nests and ranged from 0.69 to 5.7 (av. 1.5) per cent of the total weights. Lengths ranged from 49 to 111 mm (av. 70 mm). The fibers were long, twisted, and had minute side branches. Chemical preparation and microscopic examination showed that each strand was composed of numerous fine fiber-tracheids. The strands could possibly be from a variety of plants. Superficially the material resembled the core from Spanish moss (*Tillandsia usneoides*) which, of course, does not occur in the area. Most of the nests that contained these fibers were from Crawford County. The fibers were used only in nest linings. Usually no hair and few mosses were used when moderate or large quantities of fibers were used.

Deer hair.—Hair was the predominant material used in nest linings. Twenty-one nests (84 per cent) contained white deer hair (*Odocoileus virginianus*) in amounts ranging from a trace to 2.9 (av. 1.14) per cent of the total weights. A combination of mosses and hair was most commonly used in the lining. One or two nests contained a few strands of hair from other mammals.

MISCELLANEOUS.—Included under this heading are four types of materials.

One or two small feathers occurred in 3 (12 per cent) of the nests. All were apparently passerine feathers, possibly those of the Kirtland's Warbler.

Wood chips were found in 3 (12 per cent) of the nests. Amounts ranged from 1.5 to 8.8 per cent. One nest contained numerous light, sizable chips, apparently the remains of woodpecker workings.

Equisetum was found in 2 (8 per cent) of the nests. One nest contained a single short piece of the fruiting stalk of *E. fluviatile*. Another nest contained a relatively large amount (by bulk), 7.2 per cent by weight, of the vegetative portions of probably *E. sylvaticum*. These pieces ranged from 69 to 133 mm (av. 104 mm) in length.

Houstonia longifolia appeared in one nest (4 per cent). A small piece of fruiting material was found in the outer layer.

DISCUSSION

As a result of this study it is possible to conclude that nest materials are not distinct limiting factors for the distribution of Kirtland's Warbler. None of the plants identified from nests was restricted to the pine plains. Many probably occur in more dense forest stands and other jack-pine regions not inhabited by Kirtland's Warbler. However, a broader view suggests that the plants most commonly used in nests are characteristic of associations, within the pine plains, preferred by the warblers. Examination of areas that appear suitable, to us, as warbler habitat might actually show an absence of some of these important plants, thus making the area uninhabitable to the birds. This could also be one reason for the nearness of pairs within some areas rather than the birds being dispersed throughout the apparently available habitat. It is also apparent that the importance of particular species of sedges and grasses must be considered, not only with regard to the amounts used in the nests, but with consideration of their abundance in the area. With this in mind we can see that the grasses play an important dual role (1) by providing the bulk of the nest materials, and (2) by providing the major type of concealment for nests. When we consider these two points together it is obvious that the part played by these plants may indeed be important in restricting the warblers to the open, savanna-type or recently burned jack-pine areas.

Although some materials, or species of plants, appeared to be used in very small amounts (by weight) their appreciable bulk contributed significantly to the nest (e.g., deer hair, black fibers, *Equisetum*). Also some small, lightweight materials (e.g., moss sporophytes) probably required more trips by the birds to supply the amounts used in nest linings and their importance should be evaluated with this in mind.

A combination of many factors is probably responsible for the restricted range of Kirtland's Warbler. Eventually we may be able to amass all of the evidence and understand the ecological requirements of the species.

SUMMARY

1. Twenty-five nests of the Kirtland's Warbler were examined; 20 were taken apart and the materials identified, weighed, and measured.

2. The prevalence of "pine islands" is apparently necessary for the presence of breeding Kirtland's Warblers.

3. The nest is located on the ground near jack pines.

4. The nest was composed of three layers of noticeably different materials.

5. Twenty-nine species of plants were identified from nest contents. Most of these were fairly common in the pine plains.

6. The materials used in the nests were placed in 11 categories, and each species of plant is discussed as to the amounts and portions used in the nests, position in the nest, and the constancy of the species in the pine plains.

7. The abundance of sedges and grasses may be important in restricting the warblers to particular portions of the jack-pine plains. There was no indication that any one particular plant affected the distribution of the warblers. However, an association of plants, represented by those found within the nests, may have a definite influence upon the selection of nesting habitat by the warblers.

UNIVERSITY OF MICHIGAN MUSEUM OF ZOOLOGY, ANN ARBOR, MICHIGAN, 9 MARCH 1960

NEW LIFE MEMBER

We welcome Harold D. Mitchell, of Williamsville, New York, as a new life member of the WOS. A graduate of MIT, Mr. Mitchell is a retired sales engineer spending more time now on his special interests in bird distribution and in bird photography. He gives talks before various organizations and illustrates these talks with his own color slides and motion pictures. He has conducted classes for adults at the Buffalo Museum of Science, has published articles in *The Auk* and *The Wilson Bulletin*, and has read papers before the Federation of N.Y. State Bird Clubs and the AOU. Mr. Mitchell is an elective member of the AOU, a former president of the Federation of N.Y. State Bird Clubs, the Buffalo Ornithological Society, and the Buffalo Audubon Society, and a member of the Linnaean Society, Nature Conservancy, and several other similar organizations.

THE GEOGRAPHICAL AND ECOLOGICAL DISTRIBUTION OF THE BLACK SWIFT IN COLORADO

OWEN A. KNORR

THE northern race of the Black Swift (*Cypseloides niger borealis*) remained undescribed until the year 1857, at which time it was reported by Kennerly, a member of the Pacific Northwest Boundary Survey Expedition, who collected a specimen in the Puget Sound region. It seems remarkable that it could have escaped notice for so long. However, history seems to have repeated itself on a more limited geographical scale, for it was not established that the bird is a breeding species in Colorado until 1949.

The breeding range of the northern form of the Black Swift extends from southeastern Alaska southward to southern Mexico, and eastward to much of mountainous Colorado. However, within this vast area, the bird occurs only in isolated colonies due to certain ecological considerations to be discussed later. As far as the winter range is concerned, Bent (1940), who has written the only fairly complete account of the species, states that it is unknown. Whether the bird spends the winter with the resident form in Central America or goes on to South America is still to be determined.

The credit for the initial discovery of the Black Swift in Colorado goes to Frank M. Drew (1881) who collected a specimen along the Animas River a few miles east of the present site of the town of Silverton in San Juan County. He stated that it bred in this locality, but this was an inferential conclusion since he found no nests. This is further borne out by the fact that the nest and egg of the Black Swift were unknown to science until 1901, when A. G. Vrooman found the species nesting along the Pacific Coast west of Santa Cruz, California. Nevertheless, Colorado has been included in the breeding range in the AOU Check-list and elsewhere on this basis up to the present time.

The years following Drew's discovery produced very few Colorado records, some authentic and some doubtful. In 1882, Drew returned to substantially the same locality and collected a series of 10 individuals, publishing some notes on their plumages during that year. Again, in 1885, he published a short paper on the vertical ranges of birds in Colorado giving 14,000 feet as the upper limit for the Black Swift and stating that it breeds between 10,000 and 12,000 feet. Bendire (1895), in his "Life Histories of North American Birds," said that the bird seemed confined to San Juan County and mentioned Anthony's correspondence with him concerning observations of the Black Swift around Silverton in the summer of 1883; he also noted Fisher's observations of swifts of this species about the cliffs near Trinidad in July 1892, although they have not since been seen there.

In 1897, Cooke, in "The Birds of Colorado," merely repeated Drew's and Bendire's statements, managing to confuse the word "saw" with "taken" in the process, as regards Fisher's observations at Trinidad. In the third supplement to his original work, Cooke (1909) mentions that "a female in the collection of George B. Sennett is labelled as taken at Denver, June 26, 1884." Despite all efforts of the staff of the Museum of Natural History at Denver, this specimen has never been located, and Black Swifts have been recorded but once out on the plains—one was found dead near Fort Morgan in Morgan County.

The next reference to the Black Swift in Colorado was by Widmann (1911) who published a list of birds observed in Estes Park, reporting several swifts over Glacier Meadow in July of 1910. This report, along with that of Drew, is interesting in that it provided a concrete location from which to start searching for the actual nesting sites of the swift. One year after Widmann, Sclater (1912) published "A History of the Birds of Colorado," presenting a digest of the work on the Black Swift to date and contributing nothing new. Betts (1913) included the bird in his list of the birds of Boulder County on the basis of Widmann's report of the Black Swift in Estes Park (just outside the county) and some notes by Gale which were unsupported by data. In 1928, Bergtold published a small guide to the birds of Colorado in which he stated that the bird occurs "north and east as far as Golden." This is the first mention of Golden as a locality for the Black Swift, but unfortunately there are no data. This area has been the subject of considerable attention by ornithologists in recent years including three years of intensive field work by me, but the bird does not seem to occur there. Alexander (1937), who revised Betts' list of the birds of Boulder County, permitted the Black Swift to remain on the hypothetical list in the absence of the demonstrated presence of the bird in this area. Niedrach and Rockwell (1939) in their "Birds of Denver and Mountain Parks" repeated Cooke's statement of the specimen in the Sennett collection. In 1940, Bent monographed the species as completely as possible with the data then available, citing all the work done up to that time but contributing no new material so far as Colorado was concerned.

More recently, Knorr and Baily (1950) discovered two nesting colonies in the San Juan mountains of southwestern Colorado during the summer of 1949, taking the first nest and egg for the state. Encouraged by this initial success and fascinated by the bird itself, I undertook the task of determining its geographical distribution in Colorado and the ecological factors of the environment affecting this distribution, restricting the latter to the physiographic and physical aspects. At present, a comprehensive life history of the species is under way, a type of study yet to be done for this bird.

I should like to take this opportunity to acknowledge the assistance given me during

the 10 years I have been engaged in this problem. In 1949, the Denver Museum of Natural History, in the persons of Alfred M. Bailey and Robert J. Niedrach, provided the funds for the field expedition which resulted in the initial discovery of nesting Black Swifts in Colorado. The American Museum of Natural History awarded me a grant in 1951 from the Chapman Memorial Fund which permitted continuation of the rather costly field investigations, and for which I am extremely grateful. I am indebted to the staff of the Department of Biology of the University of Colorado, which awarded me a sum from the Gardner-O'Dell Scholarship Fund in 1952 to pursue my field work, and especially to Gordon Alexander, T. Paul Maslin, and Robert W. Pennak whose generous assistance brought the manuscript to its final form. Finally, the Council on Research and Creative Work of the University of Colorado awarded me a Faculty Grant to finish the distributional studies during the summers of 1958 and 1959.

FIELD INVESTIGATIONS

In order to chronicle more completely the search for the Black Swift in Colorado in recent years, it is necessary to go back to 1948. In the summer of that year, John A. Murphy and the late Robert Landberg, staff members of the Denver Museum of Natural History, were sent by the Director to San Juan County. The main purpose of the trip was to secure photographs of the Black Swift to augment the pictorial records of Colorado birds at the museum. Operating out of Silverton as a headquarters, they covered most of the territory between Red Mountain Pass on the north and Molas Divide on the south. Although they spent a number of weeks in this area, the search for the nesting sites of the swifts proved fruitless. Indeed, only a few birds were sighted during the entire period. The reasons for their failure are not clear.

It might be appropriate to mention here that the Black Swift is a very elusive bird. Its marvelous powers of flight make it extremely mobile and prohibit the establishment of any set pattern of comings and goings which often leads the observer to the nests of other species. It often feeds at great altitudes, sometimes appearing as a mere speck through a good 8× glass when directly overhead. When one considers that the bird can be easily confused with the White-throated Swift unless the light is perfect, and that the two species occur together in Colorado, the difficulties in locating a nesting site become apparent. Finally, it must be remembered that the Black Swift is far from common except on its breeding grounds, and in point of numbers of individuals probably stands near the bottom of the list among the breeding Colorado birds.

Since 1937, I had worked from time to time with Robert J. Niedrach, Curator of Birds at the Denver Museum of Natural History, and dean of Rocky Mountain region ornithologists. In the spring of 1949 he suggested that I take up the search for the Black Swift, and consequently plans were laid for a field trip to the San Juans the following summer. A. Lang Baily, a staff member of the Museum, was to accompany me on the trip. Numerous consultations were held and the literature was carefully reviewed for helpful clues. This latter point may have been overlooked by the previously unsuccessful in-

vestigators. Gradually, a method of operation evolved. In general, there are three ways to find a bird's nest. First, follow the bird to the nest. With a species as mobile as the Black Swift, this is almost out of the question without the use of hovering equipment. Secondly, be familiar with the type of locale where the bird has nested before, such as a certain species of tree or bush, and look there. Since the literature indicated that one of the keys to the problem was water, especially falling water, this seemed a step in the right direction but the checking of every cascade in San Juan County was also out of the question. Thirdly, one might stumble across the nest accidentally. The method finally adopted combined features of the first two. We decided to station ourselves where swifts had been seen on many previous occasions and to observe their flights. Then we would move in the direction of these flights in progressive stages, and when we were reasonably sure that we were in the general vicinity of the nesting site we would switch to the second method and examine all the likely spots in that vicinity.

We arrived in Silverton on 19 July 1949, and proceeded up the Animas River canyon to the approximate location of Drew's observations of 70 years before. Almost immediately three Black Swifts were observed flying up the canyon. No more were seen that day. The following day we moved up the canyon several miles above the first location and sat down to watch. After several fruitless hours five swifts appeared and proceeded to fly up and down the canyon, feeding at a considerable altitude. They finally disappeared up the canyon. We moved another mile upstream and saw more swifts feeding as before. Darkness concluded the day's observations.

Convinced now that we were on the right track, we decided to explore some of the tributaries of the Animas for possible nesting sites and to watch for any swift activity about them. The Animas Canyon had been heavily glaciated at this point, leaving many hanging valleys from which the tributary streams dropped into the canyon, producing some spectacular waterfalls. The plan was for Baily to ascend the ridge flanking Edith Gulch while I was to proceed up the canyon on foot to the ghost-town of Eureka to see if we were still too far downstream. Upon reaching Eureka I noticed five swifts orbiting the town. I climbed a rooftop for better vision and noticed that periodically they would fly up Niagara Gulch and return. Thinking I could see better from the mine dump across the canyon from the famous old defunct Sunnyside Mill, I climbed it. By this time the five swifts were joined by a sixth which apparently came down Niagara Gulch. Since Niagara was hidden from my view by the shoulder of the mountain, I left the mine dump and proceeded up Niagara Gulch. The ascent was very difficult but it soon became apparent that this was the end of the trail for Drew's swifts since the number of birds now increased to eight or nine and they were continually flying back and forth from the innermost part of the gorge. Upon reaching a point 50 yards below the falls, which have a free drop of almost 100 feet, I saw more than 12 swifts apparently flying to a large rock, which faced the falls, and clinging there. With some maneuvering I managed to assume a semi-reclining position on the

side of the gorge 12 feet from the cascade on a slippery ledge. From this position I could observe with binoculars the actions of the swifts. They flew out over the canyon, returned, and circled the cavern at the bottom of the falls. Occasionally they would land on the aforementioned rock. One landed in full view on the side of the cavern. By this time it was getting quite dark and the swifts were coming to roost. Some tried to cling to the side of the chasm near me but my presence seemed to frighten them off. Several passed within a few feet of my head. One clung to the wall about eight feet away and I shone my flashlight on it before it flew away.

The descent was negotiated with considerable difficulty. Niagara Gulch is very steep and filled with a rushing stream. The upper falls are about 1,000 feet above the valley floor and the Gulch itself is over 100 feet deep, almost vertical-sided, and drenched with spray. Moss and some small ferns constitute the plant life. No nests were actually seen, but since the swifts were coming in to roost at darkness, it seemed safe to assume that I was within several hundred feet of the nests, perhaps much closer. The colony was estimated at this time to consist of at least 12 pairs.

On the following day, 22 July, we went up Niagara Gulch to see about the possibilities of reaching the chasm at the bottom of the falls to actually view the nests. This proved impossible without pitons and rope, items of equipment we had not brought along. We tried improvising with old railroad spikes and a sledge, but the spikes would not hold. Hoping to see the nests from the side we climbed the west ridge but the extreme steepness and the rotten character of the rock prevented us from reaching a suitable position. (More recently I was able to reach the face of the nesting rock by a difficult rappel from the top of the east ridge and counted seven nests in as many cavities sprinkled across the face of the rock.)

To ensure the success of our mission, the only line of action open to us was to find another site which would be accessible to simple climbing. We investigated Arraistes, Cunningham, and Cement Creeks all in the vicinity of Silverton without success. We walked down the railroad track along the Animas south of the town for a considerable distance but saw no swifts. While checking the South Fork of the Mineral River we observed two swifts flying up and down the valley and seeming to center about Cataract Gulch. We forded the river and climbed part way up the gulch, noticing that the number of birds had increased. In addition to feeding up and down the valley, occasionally they would swing into the gulch and fly out again. One swift came in and apparently landed just above my position in the gorge. Darkness prevented further observations.

The next morning, 24 July, we returned for more investigation. There are two falls in Cataract Gulch. We planned to examine the lower falls and then

FIG. 1. Typical Black Swift nest site.

go on to the upper falls. Upon reaching the base of the lower falls we flushed a bird from a nesting hole in the rock. By climbing part way up the side of the gulch we were able to see the nest. It was about 15 feet above the pool at the base of the falls on the sheer side of the gulch and about seven feet from the falling water. The pocket in which the nest was located was about one foot wide, 10 inches high, and 10 inches deep. It appeared to have been constructed of moss and mud and the layering indicated several years of use. In the nest was a single white egg. This then was the first nest and egg of the Black Swift to be found in Colorado and vindicated Drew's assumption that the bird bred in Colorado.

We notified the museum in Denver of our discovery and they decided to send John A. Murphy, the staff photographer, to photograph the nest. Meanwhile, we took our own photographs. On the 26th of July we explored the upper falls and found two more nests, one at the base of the falls and one at the top of the falls, and on the next day we collected the nest, egg, and female from the former location (Fig. 1), the first to be taken in Colorado. They are now in the Denver Museum of Natural History collection (DMNH No. 25,551).

Both the Niagara and Cataract Gulch nesting sites were in the Upper Canadian zone about 10,000 feet above sea level. All the nests were in the close

proximity of rushing water and were subject to a cold spray, although one was drier than the rest being 20 feet from the water. The egg in the nest which was photographed felt cold to the touch after the incubating bird had been gone for some time but it later developed into a young swift. We judged the colony to be smaller than that at the Niagara location, perhaps only five pairs of swifts.

This concluded the field work for the summer of 1949, but on the trip back to Denver a stop was made in Ouray. I was surprised to see a dozen or more Black Swifts feeding over the town and I made a note to investigate Ouray County the following summer.

Limited funds reduced to a minimum the amount of field work accomplished during the summer of 1950. However, a trip was made through the San Juan Mountains in August, which resulted in the discovery of a new breeding colony in a new locality. This was near Ouray where the swifts had been sighted the year before. Employing the same method used so successfully before, the colony was located on the day of arrival, 24 August, on one of the tributaries of Canyon Creek. It was adjacent to a waterfall and there were approximately 10 pairs in the colony. The elevation was about 7,800 feet.

Recalling the fact that the wintering grounds of the Chimney Swift had remained a mystery until 1944 when some bands were recovered in Peru, and that the winter range of the Black Swift was also unknown, equipment had been brought along to band the swifts. But capturing the birds posed quite a problem. Seth Low, Director of the Bird-banding Division of the United States Fish and Wildlife Service, had informed me that the species had never been banded and he therefore could offer no help as to the matter of traps. A box to place over the nests, insect nets, and cheesecloth were all tried to no avail at both the Cataract Gulch and Ouray locations. Finally it was decided to attempt the banding at night, blinding the birds at the nest and in the roosting spots with a bright flashlight. The Ouray site was chosen for the experiment because of its proximity to the town in case of accident. Just at dusk, the climb up to the top of the gorge was made. The descent of the vertical wall was accomplished by means of a double rappel to a series of ledges and then another rappel to the nesting location. The whole procedure was complicated by darkness, wet rotten rock, and the fact that the nests were in a large chamber which was overhung by the cliff above. A flashlight held by a companion from the opposite side of the gorge illuminated a group of three nests and about six swifts, one of which was a young bird in the nest. The driving of the pitons into the rock and the swinging on the rope to get in under the overhang had not flushed them. Apparently the six-cell flashlight was bright enough to divert them. Four adults and a young bird were placed in a shirt and the descent to the bottom of the gorge was

made by finishing the rappel. The birds were banded and since the adults fly as well at night as by day, they were liberated. The young bird was placed back in the nest by my companion whom I belayed back up the wall on the rope which had been left hanging from the last piton. Thus a modest start was made in the plan to band a few swifts each summer in the hope of solving the mystery of their winter whereabouts.

On the return trip a few swifts were observed at dusk near Pagosa Springs in Archuleta County near the southern border of Colorado. The presence of the birds during the breeding season indicated the possibility of a colony in the vicinity and several were found during the summer of 1958.

During the summer of 1951 a field trip was made through the Elk, San Juan, and San Miguel Mountains of west-central and southwestern Colorado with Dr. C. W. T. Penland, Professor of Botany at Colorado College. The trip had a dual purpose: to collect specimens of the genus *Penstemon* which Penland was monographing, and to locate more nesting colonies of the Black Swift. Such a colony was discovered on the west side of McClure's Pass in the Elk Mountains west of the town of Aspen. It was of medium size (about six pairs) and was notable for the fact that the stream consisted mainly of cascades rather than the waterfalls I had come to expect. It was only the first week in August and so the eggs in the nests observed had not yet hatched. The elevation was about 8,500 feet. It was in an area unmapped by the United States Geological Survey and therefore the stream had no official name, although the few human inhabitants of the region refer to it as "West Creek." The finding of this nesting site was important in the project of mapping the geographical distribution of the swift in Colorado since it extended the known breeding range of the swifts in Colorado northward by almost 100 miles.

On the 8th of August the Ouray nesting colony was visited again, and adults were observed either incubating or covering young in the nests discovered the year before. On the 9th and 10th, many swifts were observed in the Mt. Sneffels and Camp Bird Mill area west of Ouray and although no nesting sites were located, the area was thoroughly investigated during the summer of 1952 with good results.

On the 15th of August two large colonies of at least 15 pairs were found on Bridal Veil Creek and another on Ingram Creek within sight of the town of Telluride in San Miguel County at about 10,400 feet. More colonies were suspected in Bridal Veil Basin but time limitations prevented further investigation in the San Miguel Mountains.

The two basic references in the literature concerning the occurrence of the Black Swift in Colorado are the observations of Drew in southwestern Colorado and those of Widmann in north-central Colorado near what is now Rocky Mountain National Park. As the former location had been quite fully

exploited I decided to investigate the latter. This proved to be a most vexing problem. Widmann reported that his birds were observed "over Glacier Meadow," in the vicinity of Estes Park in 1911. Park personnel knew of no Glacier Meadow. In fact, they had never seen a Black Swift. Assuming that the present day Glacier Basin was Widmann's meadow, camp was made in this area. Thus began two full weeks of dawn-to-dusk hiking and observation. Most of the area of the Park lying north of Long's Peak and east of the Continental Divide was covered. Swifts were observed at scattered locations throughout the area but they were most numerous in the territory east of Flattop Mountain and Hallett and Taylor Peaks, especially in Moraine Park, Glacier Basin, and along Mill Creek. It should be mentioned here that the character of the terrain in Rocky Mountain National Park is quite different from that of the San Juan Massif. In the Park there is only one main ridge, the Continental Divide, which runs northwest and southeast with the streams draining it at right angles. In the San Juans the mountain range is much wider with ridges and valleys running in all directions. The ridges are higher and the valleys are deeper so that the San Juans resemble the Alps more than most American mountains. Consequently, the swifts tend to fly up and down the valleys rather than over the ridges when travelling to and from the nesting sites. This is not true of the terrain east of the Continental Divide in the Park which tends to be more rolling by comparison. This made it almost impossible to establish any sort of flyways or flight patterns and thwarted the progressive following of the birds which had worked before, since they just seemed to wander over the entire area. The method which finally resulted in solving the problem consisted of plotting the daily swift sightings on a topographic map, and by the middle of the third week a funnel-shaped pattern began to emerge with the apex pointing at Loch Vale. Camp was set up at the bottom of a wet, dripping cliff in the Vale, which seemed a likely spot. The following day three nests were located by binocular from a rise opposite the cliff, two with young and one empty. The elevation was 10,500 feet. By San Juan standards the water was rather meager but there were many excellent damp nesting crannies available.

From the standpoint of the distribution study, this was the most important discovery of four years of field work, moving the breeding range north and east by 200 miles from the original Silverton location.

The summer of 1952 was by far the most successful in the search for the Black Swift in Colorado. The field work was started in Rocky Mountain National Park because it seemed that from the number of swifts observed the previous summer, more nesting colonies should exist than the small one I had found. Operating on the theory that Glacier Basin was not the "Glacier Meadow" mentioned by Widmann, I went back to the literature and found

that Widmann had been staying at the Long's Peak Inn when his Black Swift observation was made. A long-time resident of this area provided the information that Glacier Meadow had been renamed Tahosa Valley in later years. This was only four miles to the southeast of Glacier Basin but due east of Long's Peak and in an area not as yet investigated. This clue led to a series of long vigils, watching and waiting for swifts, and after about five days of work a very small colony was found on the Roaring Fork at 11,500 feet on the east slope of Long's Peak, the highest Black Swift colony located at the date of this writing. This was unusual in that timberline is some hundreds of feet lower at this latitude than in the San Juans, and the present colony was situated just at or slightly above timberline. The date of discovery was July 12th but a 100 yard-long snow bank still remained, the lower end of which was a scant 12 feet from the nest, adjacent to a small cascade. An adult was incubating at this time. The nest was kept under observation from time to time and by the 8th of August the young bird was quite visible above the rim of the nest.

Since the stream came over a glacial step on a rather broad front at this point it was necessary to enlist the aid of another person so that the main cascade and another one 70 yards to the south could be kept under observation at the same time. Douglas Alexander of Boulder kindly consented to help, and at least one and possibly more swifts were seen landing in the vicinity of the second cascade at the same time that the adults were clinging to the nest at the first cascade. However, another nest was never found although an abandoned one was observed at the second site. Whether the other birds constituted a family unit and the nest was too cleverly hidden to be located or whether they were part of a floating population coming to roost is open to conjecture. If the latter is true, the word "colonial" as usually applied to the nesting of the Black Swift is open to question.

The final observation was made at this site on the 10th of September in a swirling, early-season snowstorm. The young bird was still in the nest but was seen to be exercising its wings at frequent intervals preparatory to flying away. From the condition of the plumage and the length of the wings it was estimated that the bird had no more than a week left in the nest.

Shortly after the Long's Peak site was discovered, a short trip into the Wild Basin area resulted in the sighting of a considerable number of swifts. Wild Basin is in the extreme southeast corner of Rocky Mountain National Park and in Boulder County, as is the Long's Peak nesting site. A field trip to the San Miguel area prevented further work here but it is felt that future investigation will produce at least one more colony in this region.

Returning to the Ouray County area, five more colonies were discovered during the third week in July. They were located east of the Sneffels ghost-

town and were all of small to medium size. One colony was notable in that the volume of water present was extremely small, consisting of only a steady dripping, although roaring Canyon Creek was only several hundred yards away. The elevations of the newly found colonies were all just above or just below 10,500 feet. The old original Ouray site was checked again on the 24th of July, and of four nests visible, three had eggs and the fourth was impossible to observe because of its position.

Just prior to leaving on this last Ouray County trip, a popular article on Colorado was noticed in the *Colorado Wonderland* magazine (1952). In it was a photograph of a series of falls on Dead Horse Creek in the Glenwood Springs area which appeared to be excellent locations for Black Swift colonies. Accordingly, the return from Ouray was routed through this region and the results justified the investigation. Three colonies were discovered, one at each of the falls. Three nests were located at the upper falls, three at the middle falls, and two at the lower. The nests at the upper falls were at least 20 feet from the nearest water although they were subject to considerable spray. However, the birds at the middle and lower falls had to fly through a curtain of falling water to reach their nests, which were located under the lip over which the water rushed. At least one nest was placed within eight inches of this torrent and in order to reach it the birds would fly headlong through a thinner portion of the water curtain, make an abrupt right-angle turn, then fly parallel to the water in the narrow space between the falling water and the rock until reaching the nest, a most remarkable demonstration of aerial agility. These colonies were the lowest to be found in Colorado, the elevation being approximately 7,200 feet above sea level. Although a day's work produced only eight nests, it was felt that the total strength of the three colonies was in the neighborhood of 15 pairs. Those nests permitting direct observation still contained eggs since it was only the 26th of July.

By this time I had found that I could predict the occurrence of swift colonies from photographs or topographic maps with a fair degree of accuracy. By this means, a suitable location was indicated on Clear Creek northwest of the town of Creede in Mineral County. On the 4th of September a large colony was discovered at 10,000 feet with nests flanking both sides of a waterfall. Similarly, another swift area was discovered in the extreme southwest corner of the state. Many swifts were seen in the vicinity of Mystic Falls on the Rio Dolores, but bad weather had become general and no attempt was made to locate the nests.

On the return trip a stop was made in Ouray to investigate Cascade Falls northeast of the town. This is a magnificent cataract with a free fall of over 100 feet when the stream is running heavily. Two nests were observed, both behind the falling water. The upper nest was very high but the lower nest

permitted the observation by binocular that the young bird which it contained was still downy. Since it was the 6th of September, this indicated that there may be a considerable spread of time during which nesting is initiated. The remainder of the return trip resulted in the sighting of swifts in an entirely new area, that of Climax and Alma, but time limitations prevented the location of nesting colonies.

During the summer, in a conversation with T. Paul Maslin of the Department of Biology staff, I had described the places in which Black Swifts nest. He recalled a location in the Sangre de Cristo Mountains which seemed to fit the description, a cascade or falls on the eastern slope of the mountains in Wet Mountain Valley. Since this was more than 100 miles away from the nearest swift colony, I decided to visit it next.

On the 12th of September, the day of arrival, a heavy snowstorm hampered field work but on the following day Alvarado Creek was investigated up to about 10,000 feet. At this point a series of cascades came down through a small gorge. One nest was discovered under an overhang on a tiny ledge about 20 feet above the stream level, but it was empty, which might be expected at such a late date. About 35 feet away was an adult roosting niche, a common thing about swift colonies, identified by the droppings. No other nests were found but from the number of birds observed in the air at one time, another colony must have been in the vicinity. However, two occupied nests were found at this site in later years. This discovery was especially significant in that it was the farthest east that the Black Swift had ever been found nesting, being 105 degrees 30 minutes west longitude.

Using field methods similar to those described above, many more swift colonies were discovered in Colorado during the summers of 1953 through 1958. In Boulder County, swifts were sighted over University Camp, Caribou Ranch, Brainard Lake Basin, and Rainbow Lake Basin, all presumably from a colony situated below Arapahoe Glacier. Two more occupied nests were found at the Wet Mountain Valley site. The summer of 1958 was especially productive in closing gaps in the distribution map. Some years before, on a swift-hunting trip to Ouray, I had seen an early photograph in a hotel there of a beautiful "swifty" waterfall in the Black Canyon of the Gunnison River. A trip to the falls disclosed a small colony, the first for this general area. During the same summer three more colonies were found near Vail Pass and two more were located in the Wolf Creek Pass region.

This brought to a close 10 years of field work to determine the geographical and ecological distribution of the bird within the borders of the state. Some 15,000 miles had been traveled by automobile and it was estimated that 120 miles had been covered on foot during the course of the project.

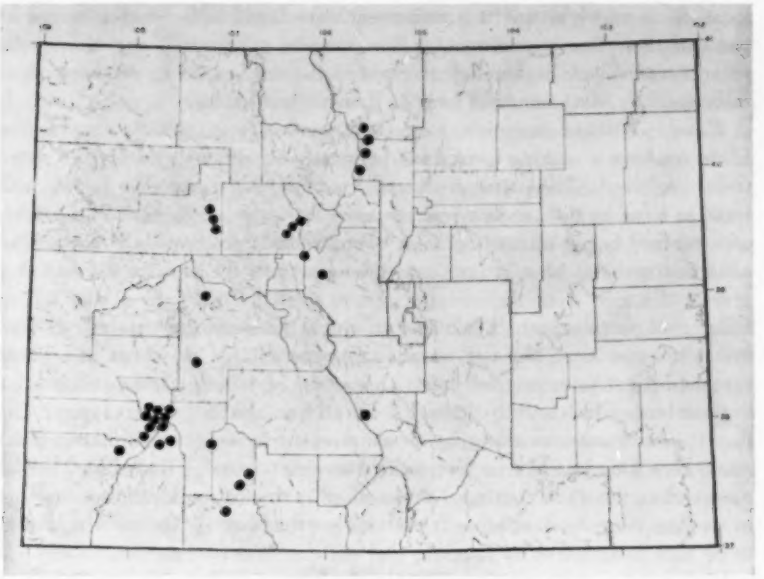


FIG. 2. Locations of active Black Swift breeding colonies and breeding season sightings in Colorado.

DISCUSSION

Geographical Distribution.—As a result of these investigations, 27 active breeding colonies consisting of approximately 80 nests were discovered at scattered locations throughout the Colorado Rockies in the counties of Larimer, Boulder, Eagle, Garfield, Gunnison, Custer, Mineral, San Juan, Ouray, and San Miguel. In addition, sightings were made in areas which should produce nesting colonies upon future field investigation. These were in Boulder, Lake, Park, Archuleta, and Dolores counties. The total area encompassed is approximately 19,500 square miles. It may be seen that the distribution brackets a major portion of the mountainous part of the state (Fig. 2), and there is little doubt that future work will show that the Black Swift will nest anywhere in the Colorado mountains that its ecological requirements are met. The nature of these requirements as established by these investigations is discussed below.

Ecological Requirements.—As the field work proceeded and the notes on the nesting colonies accumulated, an ecological pattern began to emerge. Upon analysis of these data, five physical factors were found to be present to a greater or lesser degree in all the colonies. Furthermore, seemingly suitable

locations in which no swifts were present were found to be lacking in one or more of these five requirements. They may be enumerated as follows: the presence of water, high relief as regards the configuration of the terrain, inaccessibility, darkness, and lack of flyway obstructions.

Water.—Without exception, water is present at every nesting site, varying in degree from a rushing torrent to a mere trickle, although the former seems to be preferred. The proximity of the nests to the water also varies, with some as close as eight inches and others as far away as 35 feet. The volume of water and height of free fall seem to control this positioning of nests. The attendant spray at heavily running streams permits the placing of nests at a greater distance from the running water; perhaps the roar of the falling water also plays a part. The moss of which the nests are constructed continues to grow in most cases, emphasizing the role of the spray and damp surroundings. As mentioned before, a curtain of falling water is no barrier to these birds which will fly through it to reach a suitable nesting cranny. The importance of water as a nesting site requirement is indicated in that no swift nests were found on a true intermittent stream. Even in the driest year of observation, the water continued to run at all swift nesting sites. Also attesting to the damp environment of swift colonies are the plant indicators which seem to be such hydrophiles as *Mimulus* and various ferns and mosses.

High relief.—A term borrowed from the cartographer most aptly describes the requirement that the nesting site have a commanding position above the surrounding terrain so that birds flying out from the nests on a horizontal course find themselves automatically at feeding altitude above the adjacent valley. This is to be expected since the bird habitually feeds at high altitudes and is often observed taking airborne insects which are being sucked up by the violent updrafts existing under clouds of vertical development. Some apparently suitable locations fulfilling all the other requirements but situated just at the valley floor are ignored by the swifts. The appreciation of this need for sharp contrast in the terrain surrounding swift colonies greatly simplified the search for nesting sites toward the end of the project.

Inaccessibility.—The requirement that a Black Swift nest be inaccessible to terrestrial marauders appears to be inflexible. No nest was ever found which was accessible to anything without wings. A human being with a rope or ladder is a possible exception, but at most sites this is an extremely hazardous undertaking. The fact that the bird lays only a single egg indicates that its enemies are few. However, the very inaccessibility of the nests operates as a disadvantage at times since at least one young bird has been observed to fall out of the nest to be swept away in the stream.

Darkness.—The sun rarely shines on the nest of a Black Swift. I have never found an occupied nest upon which the sun shone. Furthermore, the gloom

of the innermost recesses in the rock is preferred to lighter situations in more exposed places. The young bird invariably faces away from the light while in the nest except when anticipating the return of an adult. However, since there are more Black Swifts at nesting colonies than there are dark crannies which meet all the other nesting requirements, some nests are exposed to more light than others. An interesting borderline case was discovered in the Ouray area where a nest was placed on a sheer wall adjacent to a waterfall. As the season progressed and the sun swung lower in the sky, the sunlight crept closer to the edge of the nest. On the day that the young bird left, the sun had reached the edge of the nest and a few days later, illuminated the inside of it.

Unobstructed flyways.—As a corollary to the requirement of high relief mentioned above, the air immediately in front of a nesting site must be free of obstructions. The birds do not seem to mind flying up and down a narrow, twisting gorge, but they will not fly through a maze of tree branches to reach their nests. Many excellent sites (to the mind of the observer) were found which fulfilled all other requirements but were screened from the front by trees. No swifts were present. On the other hand, no swift colony has been found in which it is necessary for the birds to dodge trees on their way to the nests.

There may be other physical factors present which operate in the choice of nesting sites but the five mentioned above seem to be the obvious ones as established by these investigations. The impossibility of seeing the nests from above, or putting it differently, the protection from weather in the form of precipitation is another physical factor present in all cases but it is not to be ranked with the others. An additional requirement may be sound, since I have never seen, read about, or heard about a Black Swift nest which was not within range of the sound of water in motion, usually violent motion. This need not be merely a tribute to the type of environment required for a mossy nest since many permanently damp and humid crannies can be found quite remote from noisy water and which harbor no swifts. However, sound has not been generally established as an ecological factor for nonhuman animals except perhaps colonial sea birds. Future investigation will probably see the establishment of additional ecological criteria for the Black Swift. A comprehensive life history of the species is presently under way toward this end.

SUMMARY

During the summers of 1949 through 1958, field investigations were carried on to determine the geographical distribution of the Black Swift in Colorado and the ecological factors affecting this distribution. Fifteen thousand miles were traveled by automobile and 120 miles were covered on foot.

Twenty-seven active breeding colonies were located at scattered points in 10 counties

throughout most of the mountainous portion of Colorado. A nest, egg, and associated female were taken, the first to be recorded for Colorado. Additional sightings of the Black Swift were made during the breeding season in five other counties.

Five physical ecological factors were found to be present to a greater or lesser degree in all the colonies: the presence of water, high relief as regards the configuration of the terrain, inaccessibility to terrestrial marauders, darkness, and the lack of flyway obstructions in the vicinity of the nest.

It is believed that the Black Swift will nest anywhere that these ecological requirements are met.

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30 JANUARY 1960

WEATHER AND FALL MIGRATION OF HAWKS AT CEDAR GROVE, WISCONSIN

HELMUT C. MUELLER AND DANIEL D. BERGER

THE data for this report were obtained during a hawk-trapping and banding program conducted at the Cedar Grove Ornithological Station located on the west shore of Lake Michigan some 45 miles north of Milwaukee, Wisconsin. This area has been known for its spectacular hawk-flights since 1921 (Jung, 1935), and the Milwaukee Public Museum operated a hawk-banding station there for a number of years prior to World War II. Our banding program and migration studies were established in 1950 and are still in progress. The observations reported herein are from the autumns of the years 1952 through 1957.

Evidence of migration is obtained in two ways: (1) by directly observing birds in flight (visible migration) and (2) by noting the fluctuations in numbers of individuals and species in an area. Neither method offers a direct means of determining the factors operative in the inception of migration.

As Brewster (1886) and many others since have emphasized, the weather conditions at the bird's point of departure are important factors in bird migration. Unfortunately, birds have rarely been observed in the process of departing, and inferring the location of departure areas is fraught with difficulties. This is particularly true of analyses based on the presence and numbers of migrants in an area since the direction of arrival is also unknown. A concentration of grounded migrants may be the result of migrating birds encountering unfavorable weather (Bagg et al., 1950; Imhof, 1953; Dennis, 1954). Under other conditions these birds might have passed over unnoticed. Visible migration observations, on the other hand, are almost invariably conducted at localities on a coast, mountain ridge, or other "guiding line." Such observations present a biased picture of the numbers of migrants in an area and may give misleading evidence concerning the migratory direction of the birds.

The literature dealing with relationships of weather and bird migration is varied and extensive. A survey of the earlier works and a brief introduction to modern meteorological concepts can be found in the paper by Bagg et al. (1950).

Modern meteorological analysis is based on the concept of large moving air masses. The surface between two dissimilar air masses is termed a "front." At a given altitude an air mass has approximately the same characteristics throughout its extent, and frontal zones usually have about the same configuration for great distances along the front. Changes in such variables as temperature, wind direction, etc., can largely be attributed to the movements of air masses and fronts. Thus, information of the composition and

the movement of air masses is essentially a summary of the temporal and spatial occurrence of most of the meteorological variables likely to be of interest in migration-weather analyses.

Recent investigators of nocturnal migration have correlated the following meteorological factors with the arrival of migration "waves": (1) Air mass and frontal movements (Bagg et al., 1950; Bennett, 1952; Devlin, 1953; Bagg, 1958; Baird et al., 1958; Newman, 1958). (2) Following winds (Robbins, 1949; Bagg et al., 1950; Bergman, 1951; Devlin, 1953 and 1954; Raynor, 1956; Newman, 1958). (3) Temperature (Robbins, 1949; Bergman, 1951). (4) Stable (nonturbulent) air flow (Raynor, 1956). Correlations derived from telescopic observations of birds seen crossing the face of the moon generally agree with those of the students of the arrivals of migration "waves" (Lowery, 1951; Lowery and Newman, 1955).

Only a few attempts have been made in North America to correlate diurnal visible migration with meteorological variables. Hochbaum (1955) correlated major fall waterfowl flights with rising barometer, falling temperature, decreasing humidity, and northwest winds. Ball (1947) found that Red-breasted Nuthatches (*Sitta canadensis*) migrated in periods of clear weather following intervals of inclement conditions. European workers have correlated visible migration with almost all conceivable meteorological factors: e.g., barometric pressure (Griffin and Nisbet, 1953), calm weather (Williamson, 1953), wind direction (Rudebeck, 1950), temperature change (Bergman, 1951), and constant temperature (Ritchie, 1940). Jenkins (1953) correlated migration "waves" of the fall of 1951 for northwest Europe individually with several of these semi-independent variables. In addition, it must be remembered that the physiological and behavioral state of the bird underlies all migration activity and sets the basic seasonal rhythm. Farner (1955) can be consulted for a review of the work concerned with the physiological factors influencing *Zugdisposition*.

A portion of this chaos of interpretations of migration and weather patterns can be attributed to geographical differences in migration patterns, and a part to differences in behavior of the species involved. Hinde (1951) offers an explanation that simultaneously could include several weather factors. He hypothesizes that migration results from the additive effects of both the "internal drive" and the various external factors (law of heterogeneous summation, Tinbergen, 1951:81). Thus, if the internal drive is low, even an optimal combination of external factors may be insufficient to cause migration; when the internal drive is high, any one of several stimuli may suffice. Since the internal rhythm probably varies slightly from year to year, we would expect different responses to any given set of weather conditions (Nisbet, 1957).

An alternative (and, to us, more attractive) view is that the impetus for

migration lies entirely in physiological factors and that weather acts simply to aid, permit, halt, or otherwise modify the pattern of migration. The ultimate "cause" of migration undoubtedly lies in the evolutionary adaptation by selection to the breeding cycle and the availability of food, etc. (Baker, 1938; Lack, 1950). Response to a given set of meteorological conditions might be also selected for, if these conditions provide for greater survival of migrants (Nisbet, 1957).

A high correlation between a given meteorological factor and bird migration does not necessarily imply a direct causal relationship. Consider, for example, the following simplified illustration: in autumn migration usually occurs during periods of dropping temperatures and northerly winds. The birds may be responding to the temperature drop or to the effects of temperature on the food supply. Alternatively, the birds may be migrating on northerly winds simply because these following winds aid southerly passage. The correlation with temperature may thus be coincidental, or the temperature drop may serve as a "cue" announcing the onset of northerly (favorable) winds. The above can easily be further confounded by the addition of other meteorological factors.

Hawks, because of their large size and tendency to become concentrated at certain points, are extremely favorable material for a study of weather and migration. Autumn hawk-flights, studied at a number of localities in eastern North America, have been correlated with the following weather conditions: (1) west or northwest winds: Connecticut (Trowbridge, 1895, 1902); Fisher's Island, New York (Ferguson and Ferguson, 1922); Cape May, New Jersey (Stone, 1922, 1937; Allen and Peterson, 1936); Hawk Mountain, Pennsylvania (Broun, 1948, 1951); West Virginia (De Garmo, 1953); Maryland (Robbins, 1956); north shore of Lake Erie (Gunn, 1957); north shore of Lake Superior (Hofslund, 1958). (2) A low-pressure system to the north (Broun, 1951; De Garmo, 1953). (3) Decrease in temperature (Ferguson and Ferguson, 1922; Robbins, 1956). (4) Rising barometer and (5) cold front passage (Robbins, 1956). These weather conditions often occur together, and it is difficult to decide which one or several in combination are finally responsible for initiating a flight.

OBSERVATIONS

A dawn-to-dusk watch was maintained on most of 256 observation days; however, on days with little or no migration the observations often became sporadic. At the worst, observations were made with sufficient frequency to make it exceedingly doubtful that more than a dozen hawks passed by unseen on any observation day. For three of the years (1953, 1954, and 1955), observations were made essentially on every day in the period from 1 September through 25 October. In the other three years, observations

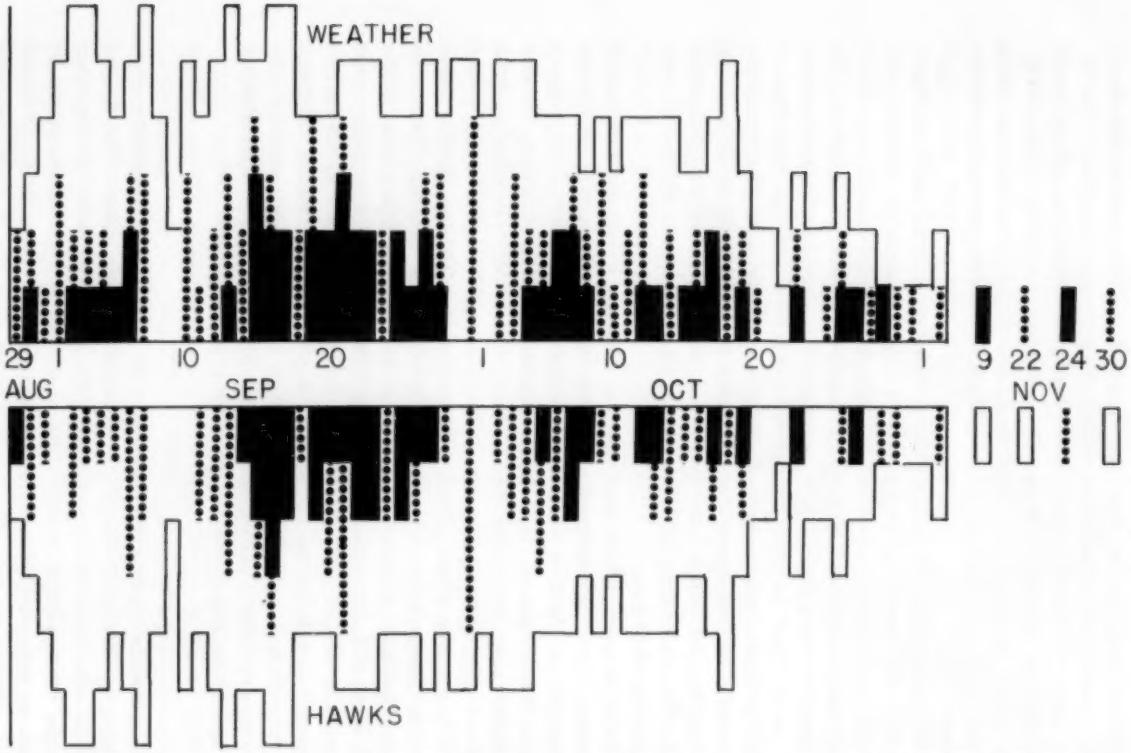

FIG. 1. Relative occurrence of observation, hawk flights, and weather suitable for hawk migration during 1952–1957. Black bars indicate number of days having Class A weather (above the date line) and the number of days having Class I flights (below date line). Similarly, dotted bars indicate Class B weather (above) and Class II flights (below). White bars indicate the number of observation days having unsuitable weather (above) and less than 25 hawks (below).

TABLE 1

NUMBERS OF HAWKS OBSERVED AT CEDAR GROVE IN AUTUMNS OF 1952–1957

Broad-winged Hawk (*Buteo platypterus*)	15,965
Sharp-shinned Hawk (*Accipiter striatus*)	8,524
Red-tailed Hawk (*Buteo jamaicensis*)	1,407
Marsh Hawk (*Circus cyaneus*)	1,115
Pigeon Hawk (*Falco columbarius*)	798
Sparrow Hawk (*Falco sparverius*)	370
Cooper's Hawk (*Accipiter cooperii*)	268
Osprey (*Pandion haliaetus*)	186
Peregrine Falcon (*Falco peregrinus*)	150
Red-shouldered Hawk (*Buteo lineatus*)	72
Rough-legged Hawk (*Buteo lagopus*)	39
Goshawk (*Accipiter gentilis*)	19
Turkey Vulture (*Cathartes aura*)	17
Swainson's Hawk (*Buteo swainsoni*)	7
Bald Eagle (*Haliaetus leucocephalus*)	6
Golden Eagle (*Aquila chrysaetos*)	2
Prairie Falcon (*Falco mexicanus*)	1
Unidentified	115
Total	29,061

were somewhat biased in favor of what we assumed to be good weather. The seasonal distribution of observation through the six years is presented in Fig. 1. Approximately 29,061 Falconiformes of 17 species were recorded. The species totals given in Table 1 are composed for the most part of actual counts, although careful estimates were made on three occasions when flights were too heavy for direct counting (these estimates are indicated in Table 2).

Four species account for more than 90 per cent of the individuals observed and largely determine the characteristics of the fall hawk-flight. Two of these, the Marsh Hawk and the Red-tailed Hawk, are well distributed throughout the entire fall, while the Sharp-shinned Hawk and the Broad-winged Hawk exhibit definite peaks of occurrence. The configuration and principal species components of the fall hawk-flight can be seen in Fig. 2. This illustration presents graphically the average number of hawks (Broad-winged, Sharp-shinned, and all other species totaled) seen per observation day for each calendar date through most of the season.

The meteorological data were taken largely from Weather Bureau publications (*Local Climatological Data* and *Local Climatological Data Supplement*) for Milwaukee, Wisconsin, 45 miles south of the observation point. Local weather publications for Madison, Wisconsin, 95 miles southwest, and for Green Bay, Wisconsin, 80 miles north, were also consulted. *Daily Weather*

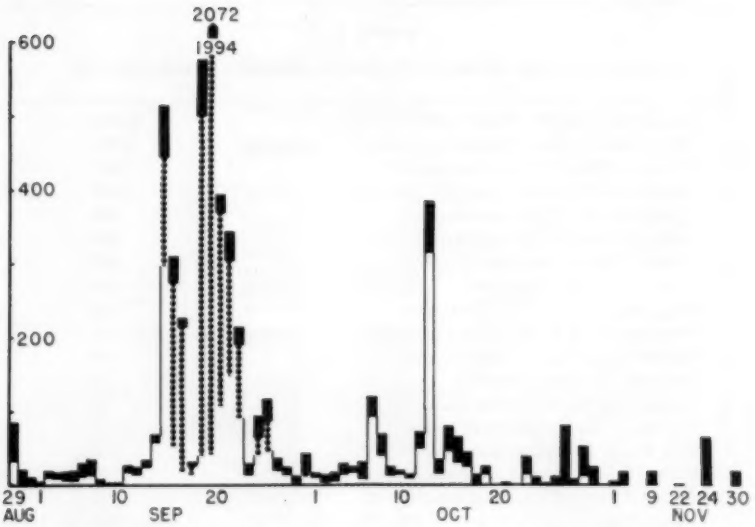

FIG. 2. Average number of hawks seen per observation day. White portion of each bar represents the number of Sharp-shinned Hawks; spotted portion, the number of Broad-winged Hawks; black portion, the number of individuals of all other species.

Maps for each of the observation days were closely examined. *Monthly Weather Review* supplied information on the movements of pressure cells. Although weather conditions were recorded at Cedar Grove, the information was not used in this report because it proved impossible to obtain consistent, accurate data with our meager equipment and varied personnel.

Although the weather conditions concerned with migration are those at the bird's point of departure, the air masses influencing the weather at the *probable* departure points of most of the birds involved in this study (i.e., to the north and west) ordinarily arrive in Wisconsin at about the same time as, or before, the birds. In the absence of more specific information regarding the areas of origin of the migrants passing Cedar Grove it would seem appropriate to restrict the analysis largely to weather conditions near the point of observation.

After a preliminary examination the observation days were placed into two classes on the basis of weather data: (A) days with westerly winds and a 1230-hour (CST) weather map similar to that shown in Fig. 3. On all these days there was a low-pressure area somewhere to the northeast of Wisconsin and high pressure to the southwest. The isobars (lines of equal barometric pressure) crossed Wisconsin on a NW–SE diagonal, and a cold

TABLE 2

LIST OF ALL OBSERVATION DAYS WITH MORE THAN 25 HAWKS AND/OR WESTERLY WINDS AT NOON

Date	No. hawks	(Broad-winged)	Wind at noon	Velocity (mph)	Wind 0600 hr.	Wind prev. day	Temp. drop	No precip.	No overcast	Days since cold front	Barometer
A. With Class A weather and more than 100 hawks											
20 Sept. 1952	129	+ 7,462*	WNW	11	+	+	+	+	+	3	R
19 Sept. 1952	129	+ 2,000*	WNW	13	+	+	+	+	+	2	R
15 Sept. 1952	1,424	+ 415*	W	21	+	+	+	+	+	1	R
13 Oct. 1955	1,484*		WNW	21	+	+	+	+	+	2	R
17 Sept. 1956	161	+ 1,015	WNW	17	+	–	+	+	+	1	R
16 Sept. 1952	296	+ 782	NW	13	+	+	+	+	+	2	S
21 Sept. 1953	101	+ 801	NW	16	+	+	+	+	+	3	R
22 Sept. 1954	583	+ 285	W	17	+	+	+	+	+	2	R
23 Sept. 1957	433	+ 394	NW	23	+	+	+	+	+	2	S
22 Sept. 1957	328	+ 483	WNW	17	+	+	+	+	+	1	R
15 Sept. 1953	285	+ 349	WNW	14	+	+	+	+	+	0	F
21 Sept. 1954	432	+ 176	WNW	22	+	–	+	+	–	1	F
20 Sept. 1953	61	+ 510	NW	12	+	+	+	–	–	2	F
21 Sept. 1952	87	+ 355	WNW	17	+	+	+	+	+	4	R
26 Sept. 1954	234	+ 159	NW	14	+	+	–	+	+	2	F
16 Sept. 1957	86	+ 195	WNW	20	+	+	+	+	+	1	R
12 Oct. 1955	260		WNW	23	+	–	+	+	+	1	F
7 Oct. 1955	244		WNW	18	+	+	+	–	–	1	F
7 Oct. 1956	243		W	15	+	+	+	+	+	1	R
25 Sept. 1953	139	+ 85	W	21	+	–	+	+	–	0	F
15 Oct. 1954	217		NW	13	+	+	+	+	+	1	R
8 Oct. 1955	204		WSW	18	+	+	+	+	+	2	R
23 Sept. 1956	117	+ 77	WNW	17	+	+	+	+	+	1	R
16 Oct. 1954	173		NW	15	+	+	–	+	+	2	F
27 Oct. 1954	158		WNW	13	+	–	+	+	+	1	R
17 Oct. 1957	145		WNW	21	+	+	+	+	–	1	R
25 Sept. 1954	139		WNW	11	+	+	–	+	+	1	R
19 Sept. 1954	135		W	28	+	–	+	+	+	1	F
27 Sept. 1953	124		WNW	5	+	–	–	+	+	1	R
23 Oct. 1953	102		NW	19	+	+	+	+	+	1	F
19 Oct. 1952	101		NW	19	+	+	–	+	+	1	S
B. With Class A weather but less than 100 hawks											
6 Oct. 1956	95		WNW	32	+	–	–	+	+	0	F
4 Oct. 1952	87		WNW	14	+	+	–	+	+	0	F
15 Sept. 1957	43	+ 32	W	15	+	–	+	+	–	0	R
4 Sept. 1953	67		NW	11	–	+	+	–	–	0	R
5 Sept. 1953	64		WNW	19	+	+	+	+	+	1	R
24 Nov. 1957	64		NW	20	+	+	+	+	+	0	R
5 Oct. 1952	63		WSW	16	+	+	+	+	+	0	R
28 Sept. 1953	63		WNW	10	+	+	+	+	+	3	F
6 Sept. 1956	61		WNW	21	+	–	+	+	+	2	R
3 Sept. 1952	59		WSW	4	+	+	+	+	+	3	R

* Estimates in part.

(Table 2 continued on next page.)

TABLE 2—*Continued.*

Date	No. hawks	(Broad-winged)	Wind at noon	Velocity (mph)	Wind 0600 hr.	Wind prev. day	Temp. drop	No precip.	No overcast	Days since cold front	Barometer
6 Oct. 1955	58		NNW	7	+	−	+	+	+	0	R
13 Sept. 1957	51		SW	13	+	+	+	+	+	2	R
29 Oct. 1954	51		WNW	20	+	+	+	+	−	0	F
2 Sept. 1952	47		WNW	24	+	+	+	+	+	2	F
2 Nov. 1952	42		WNW	12	+	−	−	+	−	0	F
30 Aug. 1955	35		W	24	+	+	+	+	+	1	F
31 Aug. 1955	30		NW	20	+	+	+	+	+	2	R
6 Sept. 1953	29		NW	2	+	+	−	−	−	2	F
17 Oct. 1954	28		NW	14	+	+	+	+	+	3	R
26 Oct. 1956	25		WNW	23	+	−	+	+	−	0	F
9 Nov. 1957	20		WNW	29	+	+	+	+	+	1	R
27 Sept. 1955	13		WSW	21	−	−	−	−	−	0	F
C. With Class B weather and more than 25 hawks											
14 Sept. 1952	298		SW	20	+	−	+	+	+	0	F
29 Aug. 1954	161		WNW	15	+	−	−	+	+	1	F
30 Sept. 1953	66	+ 19	NW	10	+	+	+	+	+	2	F
18 Sept. 1956	28	+ 44	SSW	16	+	+	+	+	+	2	R
7 Sept. 1953	65		WNW	14	+	+	−	+	+	3	R
9 Oct. 1955	62		SW	17	+	+	−	+	+	3	F
10 Oct. 1955	57		SW	15	−	+	−	+	+	4	R
7 Sept. 1956	57		NW	17	+	+	+	+	+	3	R
30 Oct. 1954	55		NNW	17	+	+	+	+	+	1	R
11 Sept. 1955	55		W	15	−	+	+	+	+	1	R
24 Sept. 1957	47	+ 5	SSW	25	+	+	+	+	+	0	R
5 Oct. 1953	50		WSW	14	+	−	+	+	+	0	F
12 Sept. 1953	49		NNW	17	+	−	+	+	−	1	F
2 Sept. 1954	45		SW	18	+	+	−	+	+	0	F
30 Sept. 1955	43		NW	15	+	+	+	+	−	1	R
6 Sept. 1955	39		WNW	15	+	−	−	+	+	0	F
30 Sept. 1957	37		WSW	21	+	−	+	+	+	0	F
4 Oct. 1954	36		NW	9	−	+	+	−	−	1	R
7 Sept. 1954	36		WNW	15	+	−	+	+	−	2	R
13 Sept. 1953	33		NNW	12	+	+	+	+	+	2	R
16 Sept. 1955	33		SSW	18	+	+	−	+	+	1	F
24 Sept. 1955	32		NW	8	+	+	+	+	+	5	R
14 Oct. 1953	32		WSW	14	+	−	+	+	+	3	F
2 Oct. 1952	31		NW	14	+	+	+	+	−	1	R
3 Oct. 1953	29		WSW	17	−	−	−	−	−	0	F
21 Sept. 1957	27		SW	23	+	−	−	+	−	0	F
30 Aug. 1953	27		WSW	7	+	+	−	+	+	17	F
30 Sept. 1956	26		NW	12	+	−	+	+	+	1	R
D. With a warm-front passage											
14 Oct. 1954	65 (51 reverse)		WSW	23	−	−	+	−	−	0	F
3 Oct. 1954	38 (4 reverse)		SSW	17	+	−	−	−	−	0	F

(Table 2 continued on next page.)

TABLE 2—*Continued.*

Date	No. hawks	(Broad-winged)	Wind at noon	Velocity (mph)	Wind 0600 hr.	Wind prev. day	Temp. drop	No precip.	No overcast	Days since cold front	Barometer
E. With Class B weather but less than 25 hawks											
19 Sept. 1953	23		NW	6	+	+	+	+	+	1	R
9 Oct. 1957	22		NW	17	+	–	–	+	–	1	R
19 Sept. 1955	22		WNW	10	+	+	+	–	–	0	F
3 Sept. 1957	21		SW	26	+	+	+	+	+	0	F
12 Oct. 1952	21		WSW	16	+	+	–	+	+	0	F
30 Nov. 1957	19		W	21	+	–	+	+	+	1	R
18 Sept. 1953	18		SW	20	–	–	–	+	+	0	F
13 Sept. 1956	16		SW	26	–	–	–	+	–	0	F
28 Oct. 1954	15		SW	26	+	+	+	+	+	0	F
23 Oct. 1954	14		WSW	12	+	–	–	+	+	9	R
16 Oct. 1955	14		NW	16	–	–	–	–	–	5	R
28 Sept. 1952	13		SSW	21	+	+	–	+	+	0	F
27 Sept. 1952	12		SSW	18	+	–	–	+	+	2	F
18 Oct. 1952	12		WSW	24	+	–	+	+	+	3	F
15 Sept 1954	11		NNW	5	–	–	+	–	–	7	S
26 Oct. 1952	9		W	12	+	–	–	+	+	2	F
1 Sept. 1952	9		WNW	8	–	–	+	+	–	1	F
14 Sept. 1955	8		WSW	9	–	+	–	+	+	0	F
8 Oct. 1953	8		SSW	17	+	–	–	+	+	2	F
4 Sept. 1955	7		WSW	10	–	+	+	+	+	6	F
10 Sept. 1954	7		NW	12	+	–	+	+	–	2	F
10 Sept. 1955	7		NNW	10	+	+	+	–	+	1	R
12 Oct. 1954	7		SSW	26	+	+	+	+	+	1	F
25 Oct. 1957	6		NNW	16	+	+	+	+	+	1	R
9 Oct. 1954	6		SW	13	+	–	–	+	–	0	F
11 Oct. 1954	6		SW	10	+	–	+	+	+	0	F
18 Oct. 1955	5		NNW	18	–	+	+	–	+	7	R
11 Oct. 1952	5		SW	14	+	–	+	+	+	3	F
1 Sept. 1953	5		SW	16	+	+	–	+	+	18	R
29 Aug. 1953	5		WSW	22	+	+	+	+	+	16	F
12 Sept. 1954	5		SW	12	+	–	+	–	–	4	R
10 Sept. 1952	4		SW	11	+	–	–	+	+	4	F
20 Oct. 1955	2		WSW	12	–	–	–	+	+	0	F
10 Sept. 1956	2		SSW	17	–	–	–	+	–	5	F
1 Sept. 1956	2		SW	17	+	+	+	+	+	1	R
3 Oct. 1952	2		SSW	21	+	+	+	+	+	2	R
19 Oct. 1957	1		NW	5	+	–	+	+	+	3	R
22 Nov. 1957	1		WSW	18	+	+	+	+	+	3	R
31 Oct. 1954	1		W	16	+	+	+	+	+	2	R
F. Without westerly winds at noon but with more than 25 hawks											
17 Sept. 1957		140	ESE	21	+	+	+	+	+	2	R
16 Sept. 1953	8	+ 129	ENE	11	+	+	–	+	+	2	R
13 Sept. 1952	91		SE	13	–	–	–	+	+	7	F
20 Sept. 1954	71		SE	12	+	+	+	+	+	2	R
26 Sept. 1953	70		SSE	18	+	+	+	+	+	1	R
13 Oct. 1954	49		ESE	13	+	+	+	+	+	2	R
12 Sept. 1952	32		ESE	15	–	–	+	+	+	6	F
11 Sept. 1952	31		SE	14	+	+	–	+	+	5	R
18 Oct. 1957	25		N	20	+	+	+	+	+	2	R

TABLE 2—*Continued.*

Date	No. hawks	(Broad-winged)	Wind at noon	Velocity (mph)	Wind 0600 hr.	Wind prev. day	Temp. drop	No precip.	No overcast	Days since cold front	Barometer
6 Oct. 1955	58		NNW	7	+	−	+	+	+	0	R
13 Sept. 1957	51		SW	13	+	+	+	+	+	2	R
29 Oct. 1954	51		WNW	20	+	+	+	+	−	0	F
2 Sept. 1952	47		WNW	24	+	+	+	+	+	2	F
2 Nov. 1952	42		WNW	12	+	−	−	+	−	0	F
30 Aug. 1955	35		W	24	+	+	+	+	+	1	F
31 Aug. 1955	30		NW	20	+	+	+	+	+	2	R
6 Sept. 1953	29		NW	2	+	+	−	−	−	2	F
17 Oct. 1954	28		NW	14	+	+	+	+	+	3	R
26 Oct. 1956	25		WNW	23	+	−	+	+	−	0	F
9 Nov. 1957	20		WNW	29	+	+	+	+	+	1	R
27 Sept. 1955	13		WSW	21	−	−	−	−	−	0	F
C. With Class B weather and more than 25 hawks											
14 Sept. 1952	298		SW	20	+	−	+	+	+	0	F
29 Aug. 1954	161		WNW	15	+	−	−	+	+	1	F
30 Sept. 1953	66	+ 19	NW	10	+	+	+	+	+	2	F
18 Sept. 1956	28	+ 44	SSW	16	+	+	+	+	+	2	R
7 Sept. 1953	65		WNW	14	+	+	−	+	+	3	R
9 Oct. 1955	62		SW	17	+	+	−	+	+	3	F
10 Oct. 1955	57		SW	15	−	+	−	+	+	4	R
7 Sept. 1956	57		NW	17	+	+	+	+	+	3	R
30 Oct. 1954	55		NNW	17	+	+	+	+	+	1	R
11 Sept. 1955	55		W	15	−	+	+	+	+	1	R
24 Sept. 1957	47	+ 5	SSW	25	+	+	+	+	+	0	R
5 Oct. 1953	50		WSW	14	+	−	+	+	+	0	F
12 Sept. 1953	49		NNW	17	+	−	+	+	−	1	F
2 Sept. 1954	45		SW	18	+	+	−	+	+	0	F
30 Sept. 1955	43		NW	15	+	+	+	+	−	1	R
6 Sept. 1955	39		WNW	15	+	−	−	+	+	0	F
30 Sept. 1957	37		WSW	21	+	−	+	+	+	0	F
4 Oct. 1954	36		NW	9	−	+	+	−	−	1	R
7 Sept. 1954	36		WNW	15	+	−	+	+	−	2	R
13 Sept. 1953	33		NNW	12	+	+	+	+	+	2	R
16 Sept. 1955	33		SSW	18	+	+	−	+	+	1	F
24 Sept. 1955	32		NW	8	+	+	+	+	+	5	R
14 Oct. 1953	32		WSW	14	+	−	+	+	+	3	F
2 Oct. 1952	31		NW	14	+	+	+	+	−	1	R
3 Oct. 1953	29		WSW	17	−	−	−	−	−	0	F
21 Sept. 1957	27		SW	23	+	−	−	+	−	0	F
30 Aug. 1953	27		WSW	7	+	+	−	+	+	17	F
30 Sept. 1956	26		NW	12	+	−	+	+	+	1	R
D. With a warm-front passage											
14 Oct. 1954	65 (51 reverse)		WSW	23	−	−	+	−	−	0	F
3 Oct. 1954	38 (4 reverse)		SSW	17	+	−	−	−	−	0	F

(Table 2 continued on next page.)

TABLE 2—*Continued.*

Date	No. hawks	(Broad-winged)	Wind at noon	Velocity (mph)	Wind 0600 hr.	Wind prev. day	Temp. drop	No precip.	No overcast	Days since cold front	Barometer
E. With Class B weather but less than 25 hawks											
19 Sept. 1953	23		NW	6	+	+	+	+	+	1	R
9 Oct. 1957	22		NW	17	+	–	–	+	–	1	R
19 Sept. 1955	22		WNW	10	+	+	+	–	–	0	F
3 Sept. 1957	21		SW	26	+	+	+	+	+	0	F
12 Oct. 1952	21		WSW	16	+	+	–	+	+	0	F
30 Nov. 1957	19		W	21	+	–	+	+	+	1	R
18 Sept. 1953	18		SW	20	–	–	–	+	+	0	F
13 Sept. 1956	16		SW	26	–	–	–	+	–	0	F
28 Oct. 1954	15		SW	26	+	+	+	+	+	0	F
23 Oct. 1954	14		WSW	12	+	–	–	+	+	9	R
16 Oct. 1955	14		NW	16	–	–	–	–	–	5	R
28 Sept. 1952	13		SSW	21	+	+	–	+	+	0	F
27 Sept. 1952	12		SSW	18	+	–	–	+	+	2	F
18 Oct. 1952	12		WSW	24	+	–	+	+	+	3	F
15 Sept 1954	11		NNW	5	–	–	+	–	–	7	S
26 Oct. 1952	9		W	12	+	–	–	+	+	2	F
1 Sept. 1952	9		WNW	8	–	–	+	+	–	1	F
14 Sept. 1955	8		WSW	9	–	+	–	+	+	0	F
8 Oct. 1953	8		SSW	17	+	–	–	+	+	2	F
4 Sept. 1955	7		WSW	10	–	+	+	+	+	6	F
10 Sept. 1954	7		NW	12	+	–	+	+	–	2	F
10 Sept. 1955	7		NNW	10	+	+	+	–	+	1	R
12 Oct. 1954	7		SSW	26	+	+	+	+	+	1	F
25 Oct. 1957	6		NNW	16	+	+	+	+	+	1	R
9 Oct. 1954	6		SW	13	+	–	–	+	–	0	F
11 Oct. 1954	6		SW	10	+	–	+	+	+	0	F
18 Oct. 1955	5		NNW	18	–	+	+	–	+	7	R
11 Oct. 1952	5		SW	14	+	–	+	+	+	3	F
1 Sept. 1953	5		SW	16	+	+	–	+	+	18	R
29 Aug. 1953	5		WSW	22	+	+	+	+	+	16	F
12 Sept. 1954	5		SW	12	+	–	+	–	–	4	R
10 Sept. 1952	4		SW	11	+	–	–	+	+	4	F
20 Oct. 1955	2		WSW	12	–	–	–	+	+	0	F
10 Sept. 1956	2		SSW	17	–	–	–	+	–	5	F
1 Sept. 1956	2		SW	17	+	+	+	+	+	1	R
3 Oct. 1952	2		SSW	21	+	+	+	+	+	2	R
19 Oct. 1957	1		NW	5	+	–	+	+	+	3	R
22 Nov. 1957	1		WSW	18	+	+	+	+	+	3	R
31 Oct. 1954	1		W	16	+	+	+	+	+	2	R
F. Without westerly winds at noon but with more than 25 hawks											
17 Sept. 1957		140	ESE	21	+	+	+	+	+	2	R
16 Sept. 1953	8	+ 129	ENE	11	+	+	–	+	+	2	R
13 Sept. 1952	91		SE	13	–	–	–	+	+	7	F
20 Sept. 1954	71		SE	12	+	+	+	+	+	2	R
26 Sept. 1953	70		SSE	18	+	+	+	+	+	1	R
13 Oct. 1954	49		ESE	13	+	+	+	+	+	2	R
12 Sept. 1952	32		ESE	15	–	–	+	+	+	6	F
11 Sept. 1952	31		SE	14	+	+	–	+	+	5	R
18 Oct. 1957	25		N	20	+	+	+	+	+	2	R

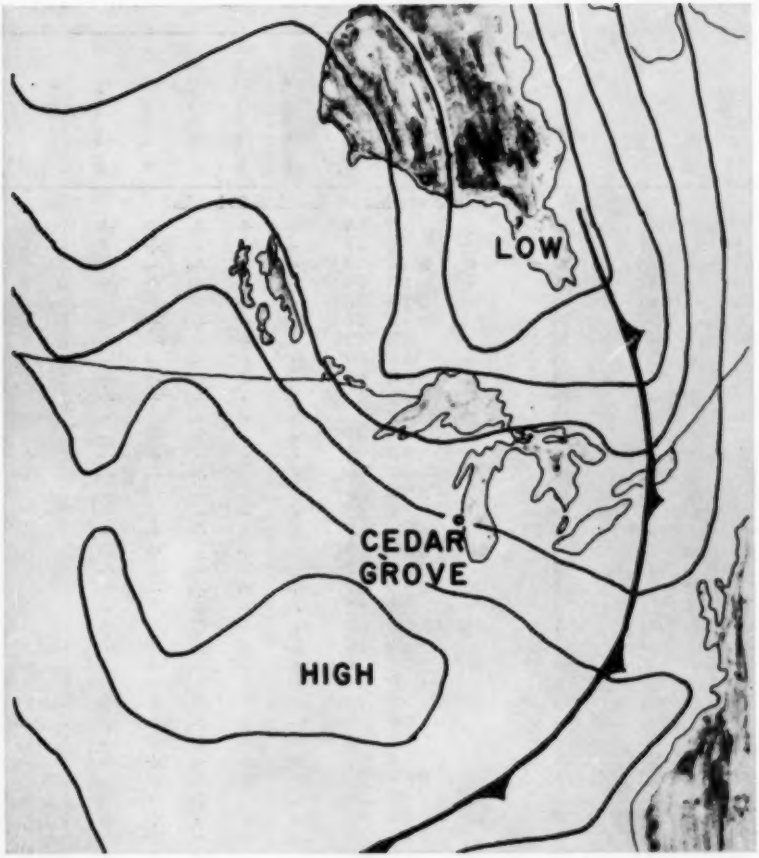

FIG. 3. An example of Class A weather. Drawn from U.S. Weather Map for 1230 hours, 13 October 1955. The line with the eastward-facing points represents a cold front; the other lines are isobars.

front lay somewhere to the south and east. (B) Days with westerly winds (between SSW and NNW) but without the above-mentioned weather map configuration. For purposes of comparing with weather conditions the observation data were grouped into two classes: (I) days on which more than 100 hawks were observed and (II) days with 25 to 100 hawks.

These four data-classes include 131 of the 256 observation days and account for 97 per cent of the hawks observed. Fewer than 25 hawks were observed

on each of the remaining 125 days, and the weather was characterized chiefly by the lack of a westerly component in the wind. To simplify the presentation of the data we have chosen to omit herein these days of poor weather and few hawks.

Figure 1 gives an indication of the correlation between flights and weather of the two classes. If the correlation were perfect, the hawk and weather data would tend to appear as mirror images on this graph. While the general correlation is good, there are numerous exceptions which call for further analysis. Table 2 lists all observation days on which at least 25 hawks were seen and/or a westerly wind was blowing. In addition, the occurrence (+) or absence (–) of various meteorological variables is indicated for each of the days. In Table 3 the classes of weather and the classes of hawk-flights are combined to yield four groups of data which are then compared with the per cent occurrence of the various factors influencing migration. These factors are individually discussed in the following section.

CORRELATION OF METEOROLOGICAL FACTORS AND HAWK MIGRATION

It must again be emphasized that migration is strongly influenced by physiological variables which act independently of any short-term fluctuations of the environment. Ninety-one per cent of the Class I flights and 93 per cent of the hawks seen in this study were observed in the period 14 September through 20 October. Before 14 September and after 20 October good weather often fails to produce a good hawk flight; during the period hawks fly even if weather only begins to approach the optimum (see also Table 3, line 1).

Wind direction.—This yields perhaps the best correlation with hawk migration at Cedar Grove. Eighty-three of the 92 Class I and Class II flights occurred on days with westerly winds at noon. In six of the nine exceptions the wind was westerly earlier in the day, and the flight occurred largely before the wind shifted.

Westerly winds apparently cause southward-bound birds to drift eastward until they encounter the shore of Lake Michigan. Since hawks are reluctant to fly out over this 70-mile-wide expanse of water, their easterly drift is arrested, and the birds become concentrated along the lake shore. The lake shore acts as a "guiding" or "leading" line (*Leitlinien* of Geyr von Schweppenburg, 1929). The birds observed moving south over Cedar Grove at any given time will be those which have encountered this guiding line at some point to the north. If we assume that the hawks are more or less randomly scattered on a broad front before they encounter the guiding line, it follows that the longer the period of westerly winds the greater the number of hawks observed at a point on the guiding line. Easterly winds, on the other hand, would drift birds *away* from the lake shore.

TABLE 3

PER CENT OCCURRENCE OF INFLUENCING FACTORS FOR EACH CLASS OF DATA

Weather class	A	A	B	B
No. of hawks	> 100	< 100	> 25	< 25
No. of days	31	22	28	39
Within 14 Sept. to 20 Oct. inclusive.	93	36	65	51
With westerly winds at 0600 hr.	100	91	86	77
With westerly winds previous day.	77	68	61	46
With more than 100 hawks previous day.	35	5	18	3
With noon winds W to NW.	97	91	43	26
With W winds persisting since cold front.	97	91	67	41
With noon winds of velocity > 10 mph.	97	86	86	87
With noon winds of velocity > 15 mph.	68	55	61	54
With temperature drop.	84	77	64	59
Without overcast.	84	68	75	74
Without precipitation.	93	86	93	85
With rising or steady barometer in prev. 24 hours.	68	55	50	41

Good migration days almost invariably have westerly winds from daybreak on, and often the wind is also westerly on the preceding day (Table 3, lines 2 and 3). Exceptionally good flight-days are almost invariably preceded by a few hundred birds on the previous day. More than one-third of all Class I flights occurred the day after another Class I flight (Table 3, line 4). However, the frequent changes which characterize autumn weather rarely permit more than two or three consecutive Class I days.

TABLE 4

CORRELATIONS OF HAWK MIGRATION AND VELOCITY OF THE WESTERLY COMPONENT OF THE WIND

Velocity (mph) of westerly component	Wind direction						
	NNW	NW	WNW	W	WSW	SW	SSW
A. Total number of hawks observed							
> 20	—	—	1,030	2,233	17	—	—
15–20	—	—	2,797	918	283	52	—
10–15	—	2,395	13,262	139	183	514	—
< 10	224	2,713	218	—	101	77	199
B. Average number of hawks per observation day							
> 20	—	—	258	558	9	—	—
15–20	—	—	311	306	71	17	—
10–15	—	218	1,020	46	26	64	—
< 10	28	194	55	—	25	13	25

To illustrate the effects of wind drift let us consider a hypothetical hawk with the following characteristics: (1) a constant flight speed of 20 mph, (2) a constant flight direction (directly south), and (3) free drift with the wind. A SSW wind of 20 mph would arrest the southward progress of this hawk 18.5 miles each hour; the net southward speed of the bird would be 1.5 mph. The hawk would require 66.7 hours to move a distance of 100 miles to the south. Eastward drift would amount to 7.7 mph or 514 miles during the time required to move 100 miles southward. Distances of eastward drift for other wind directions (velocity 20 mph), derived similarly, are: SW, 283 miles; WSW, 150 miles; W, 100 miles; WNW, 67 miles; NW, 41 miles; and NNW, 20 miles.

If drift were solely responsible for the hawk migrations observed at Cedar Grove, more birds would probably be seen on SW winds than on NW winds. However, the opposite is true for most migration occurs on days with W or NW winds. Table 4 shows the correlation between wind direction, velocity of the westerly component of the wind and hawks seen per day.

Observations at Duluth, Minnesota (Hofslund, 1958), and on the north shore of Lake Erie (Gunn, 1957) show that the bulk of hawk migration occurs on northerly and westerly winds. The topography and *Leitlinien* in these localities is such that one would expect concentrations of migration on northerly, as well as westerly, winds. The only hawk migration report from the east shore of Lake Michigan known to us was on a northeasterly wind (Smith, 1904).

Since fall hawk migration apparently occurs most frequently on westerly or northerly winds, it is reasonable to suggest that following winds initiate hawk migration. However, westerly and northerly winds are associated with a complex of meteorological factors, and a review of these is necessary before a final judgment can be advanced.

Cold fronts.—The passage of a cold front in the northern United States is characterized by a rather sudden change in most measurable meteorological variables. The temperature falls, the sky rapidly clears, the humidity drops, the barometer reaches a low point and begins to rise, and the wind shifts from southerly to westerly or northerly. In fall, westerly and northwesterly winds are almost invariably associated with a recent cold front passage. Depending on the speed of movement and the paths taken by the large air masses which govern our weather, the wind may swing slowly to southwest after frontal passage, or it may shift clockwise to the south. Thus, southwesterly winds usually occur just before or several days after a cold front. More than 92 per cent of the migrant hawks observed at Cedar Grove passed on 84 days which were characterized by westerly to northwesterly winds following a cold front. Fewer than 4 per cent of the total number of hawks observed passed on 35 days with other westerly winds. Line 6 of

Table 3 gives the per cent of the days of each data-class on which the wind remained westerly or northwesterly after the passage of a cold front. Class A weather, as defined above and illustrated in Fig. 3, implies the recent passage of a cold front. In fact, the existence of westerly winds shortly after the passage of a cold front almost necessitates a weather map similar to that of Fig. 3. Three Class I flights of 35 did not have this weather map configuration, but they did have a recent cold front passage and the migration occurred in the period before a wind shift.

One Class I flight (14 September 1952) occurred in part *before* a cold front passage. The flight came at the end of an extremely atypical period of weather and hawk migration. A cold front approached Wisconsin from the northwest and became stationary just north of Lake Superior in the evening of 8 September 1952. The front remained in approximately the same place until 13 September when it began to move northward as a warm front. A new cold front moved in from the west and passed Cedar Grove at 1430 hours on 14 September. The hawk-flight began on 11 September when 31 birds were observed on a southeast wind! Even though the easterly wind persisted through 13 September, the hawk-flight slowly increased in magnitude: 32 birds on 12 September and 91 birds on 13 September. The flight continued unabated on 14 September when the cold front and an attendant rain squall scarcely interrupted the movement of 298 hawks (one bird was actually observed flying through an intense thundershower). Class A weather prevailed on 15 September, and 1,839 hawks, including a record count of 1,219 Sharp-shinned Hawks, passed over Cedar Grove.

Both the pre-frontal flight of 298 hawks and the smaller flights on the southeast winds of the preceding days are unique to our experience. We propose that the hawks began migrating in Canada with the arrival of the 8 September cold front. The birds continued south after the front halted and began to arrive in east-central Wisconsin on 10 and 11 September. In the region of Green Bay they encountered SSW to WSW winds and were drifted east to the shore of Lake Michigan. Somewhere in the 80 miles between Green Bay and Cedar Grove the wind became SE, but a few birds apparently continued to follow the lake shore at least as far south as Cedar Grove in spite of the easterly winds. On 14 September the winds were SW at both Cedar Grove and Green Bay, and the hawk-flight increased correspondingly.

Warm fronts.—The northward movement of a well-developed warm front in autumn is a rarity in Wisconsin. Only six of the 256 observation days were characterized by such a phenomenon. One of these, 14 October 1954, resulted in the only observed autumn occurrence of a reverse migration of hawks at Cedar Grove. Fifty-one of the 65 hawks seen that day were moving northward. At 0030 hours on this date the weather map showed a warm front about 50 miles south of Cedar Grove. On the 1230-hour weather

map the warm front had progressed to the top of the lower peninsula of Michigan, and an eastward-moving cold front had just passed Cedar Grove. The wind was southerly all morning, shifting to westerly at noon, when the cold front passed. All birds were observed in the afternoon. The hawks probably began moving northward after the warm front in the morning but were not drifted against the lake shore until the wind shifted to the west. Once started north they apparently maintained this direction even after the cold front passed. The next day produced a southward migration of 217 hawks.

A second warm-front-date, 3 October 1954, differed considerably in the time of passage and the speed of movement of the front. The 0030-hour weather map showed a warm front a short distance south of Cedar Grove. This front remained essentially stationary and did not pass Cedar Grove until about 1130 hours. Twenty-seven birds moved southward on westerly winds before the warm front passed; four of 11 hawks after the front were moving northward. A cold front passed in the afternoon, and the following day 36 hawks moved southward on a west-northwest wind. Overcast skies persisted on both the above warm-front-days; the remaining four days with warm fronts were characterized by easterly winds and/or partly cloudy skies, and little or no hawk migration was observed.

Drost and Bock (1931) in analyzing cases of reverse fall passerine migration in Europe suggest that overcast skies may have hampered the birds' navigational ability. This idea gains support from the recent works of Kramer (1948, 1952), Kramer and Riese (1952), and Bellrose (1958), demonstrating sun-compass orientation in three orders of birds. It is reasonable to propose that on 14 October the hawks began migration in response to the warm front, and in the absence of orientation clues from the sun they flew northward with the following winds. It must be emphasized that this is not to be taken as an explanation for all reverse migration. Reverse flights often occur on clear days in spring at Cedar Grove. Fall reverse migration, because of its extreme rarity, probably merits some such special discussion as is given above.

Updrafts.—Hawks probably make considerable use of vertical air currents in their migratory passage. It is thus advantageous for the hawks if migration occurs when updrafts are available. In the lower layers of the atmosphere vertical winds are due largely to deflection of horizontal winds (as on the Appalachian ridges) and to heating of air at the surface of the ground. The latter process is at a maximum on clear days when the sun is producing a maximum of heating of the ground and when the overlying air mass is relatively cool. The clear skies and lower air temperatures usually associated with the air mass following the passage of a cold front thus provide optimum conditions for the formation of updrafts.

These updrafts tend to form into organized patterns. Under near-calm conditions these vertical currents take the form of large, columnar, chimney-like updrafts. If a horizontal wind exists, the resulting shear tilts the updrafts downwind, and with increasing wind velocity the columnar structure is disrupted. Laboratory investigations (Phillips and Walker, 1932; Graham, 1934) have shown that within a certain range of horizontal shear the convection patterns are organized into longitudinal "strip-like cells" of alternating updrafts and downdrafts.

Observations of gull-soaring over the North Atlantic (Woodcock, 1942) indicate that similar patterns of thin vertical sheets of rising air apparently occur in the free atmosphere at horizontal wind velocities of approximately 15 to 28 mph when the surface water temperature is at least 4°C higher than that of the overlying air. Woodcock noted that gulls soared in circles when the horizontal wind velocity was less than 15 mph. When the wind velocity ranged between 15 and 28 mph, the gulls soared in straight, narrow lines headed upwind. The rate of ascent was usually greater than that with circle-soaring. No soaring of any kind was observed at winds in excess of 28 mph, suggesting that convection patterns were disrupted or updrafts were of insufficient lateral extent to be useful to the gulls.

The pattern of updrafts over a land surface may be considerably different from that given above. Current theory holds that convection over a terrestrial surface takes the form of discrete bubbles or chains of bubbles of rising air (Ludlam and Scorer, 1953). Further differences would result from the irregularities of topography and varying heat capacity of a land surface. Unfortunately, we were unable to find any information about the organization and structure of updrafts in the atmosphere within a few hundred feet of the soil surface. At higher levels, however, both updrafts of the columnar or bubble form and of the longitudinal-strip type are found (Slater, 1947; Lange, 1940). It is interesting that much of the information available on updraft structure has been gathered by sailplane pilots whose numerous flights of over 100 miles are adequate evidence of the possibilities of soaring flight.

In the absence of information to the contrary, we suggest that updrafts at low altitudes over a land surface are to some degree organized in a form similar to that given by Woodcock (1942). Thus, we expect that longitudinal updraft cells exist over a suitably warm ground surface at horizontal wind velocities between approximately 15 and 28 mph. If the updrafts in these cells are of sufficient strength, a migrating hawk would be able to fly up- or downwind at considerable speed with minimal effort. Cross-wind flight could be sustained by remaining in areas of updraft as long as possible and moving through downdrafts at high speeds.

Thus, the observed correlation of hawk migration with cold fronts and

with winds of 15 to 25 mph may be simply a correlation with optimal soaring conditions. The hawk-migration observations of Rudebeck (1950) in Sweden and Holstein (1946) in Denmark also seem to show better correlation with the occurrence of weather conducive to thermal updrafts than with any other meteorological factor.

Wind velocity.—There is an easily discernible difference in the reactions of birds of the genus *Buteo* and those of other hawks in regard to wind velocity. Buteos, particularly the Broad-winged Hawk, characteristically ascend circularly to great heights on a columnar updraft or rising bubble of air, then glide off in a line until a new updraft is encountered. High wind velocities break up the formation of such updrafts and inhibit *Buteo* migration. Optimum wind velocities for these soaring hawks at Cedar Grove range from 10 to 15 mph. The birds undoubtedly will fly at lower wind velocities, but the *Leitlinien* effect is rapidly reduced as wind speed decreases, and no concentrations are formed along the lake shore. The other species of hawks occur in greatest numbers at wind velocities of 15 to 25 mph (Table 3, lines 7 and 8). Winds greater than 30 mph seem to progressively inhibit all hawk migration. The Broad-winged Hawk is listed separately in Table 2 because of the above-mentioned differences in reaction to wind velocity.

Temperature.—Bird-migration might well be related to temperature change, but an uncomplicated analysis of the role of this factor is impossible. Temperature change is markedly effected by a number of seasonally independent factors. Cloud cover, for example, inhibits both nocturnal cooling and diurnal warming, severely damping variations in temperature. Wind disrupts the formation of inversions, and thus prevents extreme nocturnal cooling of low-lying areas. Thus, the influence of a moving air mass on local temperature can be completely masked or markedly exaggerated by various local conditions. The correlations were therefore not so good as conceivably might be expected, but it is possible that no better relationship exists since the aforementioned variations may well confuse the bird as well as the investigator.

Correlations of migration and daily temperature change were attempted for difference in (1) average, (2) maximum, and (3) minimum temperature from the corresponding datum for the previous day. Decrease in minimum temperature yielded the best correlation with migration, and it alone is listed in Tables 2 and 3. Temperature drop is indicated by (+) and increase or no change by (–) in Table 2.

Two seasons (1952 and 1955) were analyzed in regard to short-term temperature changes. The greatest observed drop in temperature in an hour's interval during the 24 hours prior to noon was tabulated for each observation day and compared with the number of hawks observed. A second method, utilizing the temperature change over six-hour intervals, was also attempted.

TABLE 5

CORRELATIONS OF TEMPERATURE AND MIGRATION

Weather class / No. of hawks	A >100	A <100	B >25	B <25
Mean of departure of average daily temp. from normal.	−2.00	−2.59	−0.74	+1.82
Mean of departure of minimum daily temp. from average of minimum for previous 5 days.	−4.84	−6.79	−4.68	−1.19
Mean of departure of average 0030-hr. temp. for Duluth, Wausau, and Escanaba from same datum of prev. day.	−2.52	−1.44	−0.88	+0.44

Temperature changes between 1200–1800 hours and 1800–2400 hours of the previous day and between 0000–0600 hours and 0600–1200 hours of each observation day were tabulated. Adjustments for the normal daily temperature cycle (warming in forenoon, cooling in evening) were made in the following manner: mean temperatures of 0600, 1200, 1800, and 2400 hours were calculated for each month of observation, and the average change for each six-hour interval was determined. The net temperature change for a six-hour interval on a given day was obtained by subtracting (or adding) the average change. No reasonable correlation was found between hawk migration and these short-term temperature changes.

Finally, we tried to correlate migration with (1) the departure of the average daily temperature from normal for each day, (2) the departure of the minimum daily temperature from the minima for the previous five days, and (3) the departure of the average of 0030-hour (CST) temperatures for Duluth, Minnesota, Wausau, Wisconsin, and Escanaba, Michigan, from the corresponding datum of the previous day. The data for these considerations are given in Table 5. In each case, temperatures averaged two to three degrees lower for days on which more than 100 hawks were observed.

Although hawk-flights usually occurred after a drop in temperature and on days with relatively lower temperatures, the correlations do not appear to be of sufficient magnitude to warrant a migration hypothesis based exclusively on temperature. Trowbridge (1902) came to similar conclusions in his analysis of Connecticut hawk-flights.

Precipitation and overcast.—Table 3 (lines 10 and 11) lists the per cent occurrence of lasting overcast or appreciable precipitation in the morning hours for each class of data. Since the skies usually clear rapidly after a cold front has passed, it is interesting to note that migration occurred on some of the few days on which overcast skies persisted and some precipitation

was recorded. Extended heavy rains usually ended migration, but occasional brief showers often hardly interrupted a flight.

Cloudiness reduces insolation of the ground and hence lessens air-ground temperature contrasts. This reduces, but does not necessarily eliminate, the production of updrafts. If the ground is sufficiently warmer than the invading cold air mass, updrafts will result without the aid of insolation.

Barometric pressure trends.—The only barometer-readings readily obtainable for the entire period of this study were those recorded at six-hour intervals in the *Local Climatological Data Supplement* for Milwaukee, Wisconsin. A correlation of these data with hawk counts indicates that hawks migrate more often on rising or stable barometers than when the pressure is decreasing (Table 3, line 12). This relationship is probably secondary and incidental to other factors related to the movement of the cold front. There is no sensory mechanism known by which a bird could determine absolute pressure, and there is no evidence that birds can detect the slight changes in barometric pressure that occur in nature over a period of a few hours. A bird flying from the ground to the tree tops would be subjected to an air pressure change of 0.05 to 0.08 inches of mercury; an atmospheric pressure change of this magnitude rarely occurs in an interval as short as an hour.

Air-mass movements.—A careful study of the origins and paths taken by the centers of both high- and low-pressure cells prior to their entry into the western Great Lakes area yielded no reasonable correlation with migration. The air masses in which migration occurred were almost invariably of "polar" origin, i.e., the origin was in colder, more northern regions. Beyond this restriction, it apparently made little or no difference as to where the air mass originated or as to what path it pursued before it arrived in the upper middle-west.

SUMMARY AND CONCLUSIONS

Daily counts of autumn-migrating hawks were made on 256 days in the years 1952 through 1957 at Cedar Grove, Wisconsin. Most of the migration occurred between 14 September and 20 October. More than 92 per cent of the migration occurred on 84 days characterized by westerly winds and the recent passage of a cold front. Westerly winds serve to concentrate migration along the guiding line formed by the west shore of Lake Michigan.

The fact that correlations of hawk migration with individual factors associated with frontal passage are not so good as correlations with cold fronts per se suggests that these factors act additively in effecting migration. An alternative suggestion is that weather affects migration indirectly in that it acts to modify, not produce, migration. We propose that the relation of fall hawk migration to cold fronts and winds of 15–25 mph is, simply, a correlation with the occurrence of conditions suitable for updraft formation and, hence, with good conditions for soaring and gliding.

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SONG VARIATION IN A POPULATION OF MEXICAN JUNCOS

PETER MARLER AND DONALD ISAAC

THE variability of bird songs is familiar to all field ornithologists. Geographical variation in particular has received considerable attention partly for its intrinsic interest and partly because its understanding promises to throw some light on the role of reproductive isolating mechanisms in speciation.

However, the problem of describing geographical variation in song is complicated by the excessive variability which we sometimes find within a single population of birds, as in the European Chaffinch, *Fringilla coelebs* (Marler, 1952). An understanding of the extent and significance of this local variation is a prerequisite for analysis on a geographical scale. During an expedition to Mexico in 1958 an ideal opportunity was found for such study in the pine woodlands near El Salto in Durango. Mexican Juncos (*Junco phaeonotus*) are very common there, and the habitat is uniform. It was possible to record songs from a large number of males—67 songs in all from 63 males—within a restricted area of about one square mile. This sample of songs from a single population is much more variable than in other species we have studied such as the Chipping Sparrow and the Brown Towhee (Marler and Isaac, 1960*a*, *b*). Our intention in this paper is to try to document this variation, both in terms of the over-all characteristics of the song and also with regard to the structure of the component syllables. We thus hope to determine which characteristics persist throughout this variability, providing the basis for whatever species-specific properties the song of the Mexican Junco may have.

METHODS

The songs were recorded in the field with a Magnemite 610 E tape recorder at a tape speed of 15 inches per second with an Altec 633A microphone mounted in a parabolic reflector. A Madison Fielding Micamp was used in the microphone circuit. In the laboratory the tapes were played back on a Viking 75 tape deck modified to operate with a tape speed of 15 inches per second. Analyses were made with a Kay Electric Company Sonagraph and amplitude display unit using the wide band-pass filters and the "high-shape" setting in all cases. The syllable analyses are based on ink tracings made directly from the sonagrams on tracing paper. Figures 1 and 6 are from photographs of tracings of this kind. The recordings were made between 29 June and 3 July 1958, within an area of approximately one square mile within short walking distance of a camp in the pine forests to the northwest of El Salto, in Durango, Mexico. Two or three examples of the songs of each bird were recorded. From each of these samples one example of each song

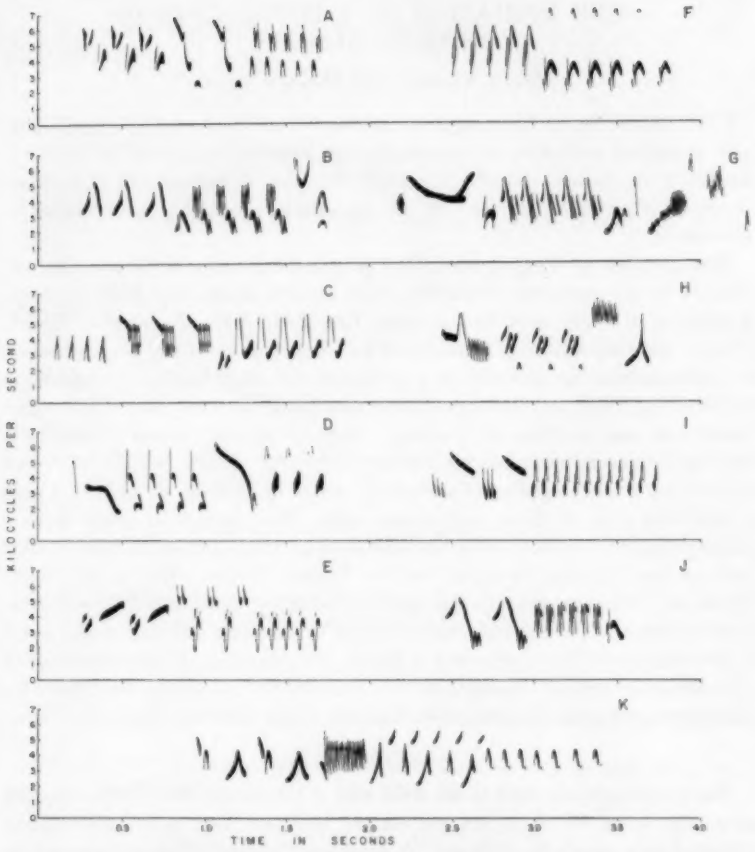


FIG. 1. Sonagrams of songs of 11 individuals selected from recordings made near El Salto, Durango. A–E: These songs represent the most common condition (based on such characteristics as over-all duration, number of syllable types per song, number of trills per song, etc.). F–K: These songs represent extremes as follows: F—few syllable types; G—many syllable types; H—few trill syllables; I—many trill syllables; J—a short song; K—a long song.

pattern recorded was selected for analysis. Data on the frequency and temporal characteristics of the songs were read off on a graduated clip board (see Marler and Isaac, 1960*a*). Unless otherwise stated, the data are presented as arithmetic means plus or minus one standard deviation.

TABLE 1

FREQUENCY OF DIFFERENT TYPES OF SONG, CLASSIFIED ACCORDING TO POSITION AND NUMBER OF TRILLS AND PHRASES*

One-trill songs		Two-trill songs		Three-trill songs		
4	aBc	13	AB	5	ABC	
3	Ab	12	ABc	2	AbCD	
		9	AbC	2	ABCd	
		7	AbCd	1	ABcD	
		4	aBC	1	AbCDe	
		2	aBcD	1	ABcDe	
		1	aBCd			
Totals 7		48		12		67

* Trills are represented by capital letters, and phrases by small letters.

GENERAL DESCRIPTION OF THE SONG PATTERN

In a sustained bout of singing, a bird delivers one pattern several times with little variation, then switches to another and then returns to the first, and so on. In most cases we have recorded only one song pattern from each bird. Mexican Juncos have a complex song, considerably more elaborate than the simple trill of the Oregon or Slate-colored Juncos. Although the song is about the same duration as in other juncos, it is built from several syllable types instead of just one. Each male has a repertoire of several song patterns, two or three being an average estimate from field observations.

Song analyses of this sort pose a problem in terminology. For sake of clarity in the following descriptions and discussions we have used the terms *note, syllable, trill,* and *phrase.* These terms are useful in this particular case, but may not have any general application. In fact it may be difficult or even impossible to use the same terminology for other types of songs, such as those of some of the more versatile singers (thrushes, etc.). Until such songs are analyzed and a suitable terminology derived, the terms used herein should not be extended beyond their present context.

In the terminology we use for the different parts of the song, as revealed in a sonagram, the basic units are the *notes,* each of which is one continuous vocal utterance. A single note may be modulated in frequency or amplitude in a complicated way, to form quite an elaborate unit. Any break in continuity is regarded as the end of a note. Notes are often arranged in groups to form more or less coherent units, which are the *syllables.* These are not always easy to identify with certainty, except when they are repeated consecutively two or more times, to make a *trill.* When they are not repeated in this fashion, their identification becomes more arbitrary (although the term is still useful).

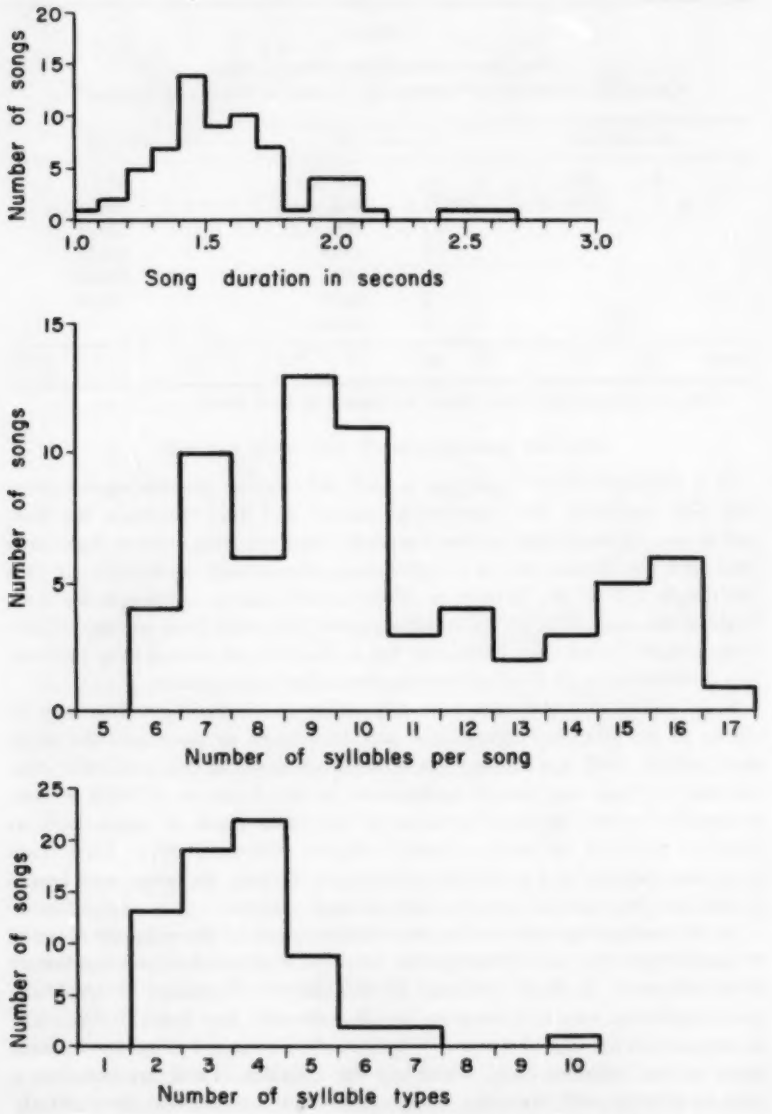


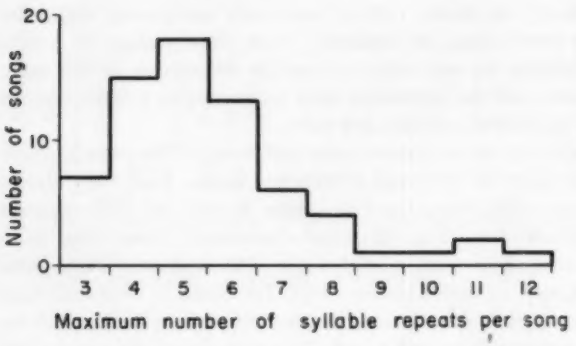
FIG. 2. Frequency distributions of song duration, number of syllables per song, and number of syllable types per song.

Our final subdivision is a *phrase*, one or more such unrepeated, dissimilar syllables which, in these songs, are separated from other phrases by a trill. Using these subdivisions we can make a complete description of the song, beginning with its over-all characteristics, then proceeding to a finer analysis of the structure of individual syllables and notes.

On careful examination we can discern some patterning in the ways in which the syllables are arranged in the songs of different birds. Each song always includes one or more trills. In a few cases there is only one trill sequence (e.g., Fig. 1H), usually two (Fig. 1B), and occasionally three (Fig. 1A). These trills are arranged in many varied ways. The song may begin with a trill (Figs. 1A, B, etc.) or with a phrase (Figs. 1D, G, etc.). Two trills may follow immediately on each other or may be separated by a phrase. And the song may or may not terminate with a trill. The majority of the songs (49) had at least one phrase. Table 1 shows that the number of basic parts in the song can vary through two (16 songs), three (34 songs), four (15 songs), and five parts (2 songs).

The average duration of all songs (Fig. 2) was 1.63 ± 0.29 seconds. Thirty-five unbroken pauses between consecutive songs in the recordings averaged 5.4 ± 1.4 seconds. Thus, at a rough estimate, these birds spend about 23 per cent of their singing time actually in song. The number of syllables in the song also varies, from 6 to 17, with an average of 10.1 ± 2.9 (Fig. 2). In neither respect is this variability excessive, as compared with the Brown Towhee, in which song duration varies similarly, and the number of syllables per song is considerably more variable (10.4 ± 4.5, Marler and Isaac, 1960*b*). As in the towhee, there is a rough correlation between these two measures, shorter songs tending to have fewer syllables than longer ones, but there are many exceptions. One song with 6 syllables, for example, was longer than another with 14 syllables.

There is also a diversity of syllable types in each song (Fig. 2) but the number per song, 3.7 ± 1.4 is relatively consistent. Thus, each song always has at least two syllable types, and rarely has more than five. As pointed out earlier, some of these are given only once in a song, while others are repeated. We can express the amount of repetition in the ratio of the number of syllables to the number of syllable types (Fig. 3). For this sample the value is 2.97 ± 1.05. This is a much lower figure than we would obtain for the Chipping Sparrow or the Brown Towhee, but, nevertheless, the trills are a prominent characteristic of Mexican Junco songs, and merit closer attention. The trills make up the greater proportion of each song, contributing 8.5 ± 2.7 syllables and a duration of 1.24 ± 0.29 seconds, as compared with 0.40 ± 0.25 seconds from 1.7 ± 0.9 phrase syllables. The lower variability of the figures on trills, particularly the duration, emphasizes their importance as a basic characteristic of the song, as compared with the less regular phrases.



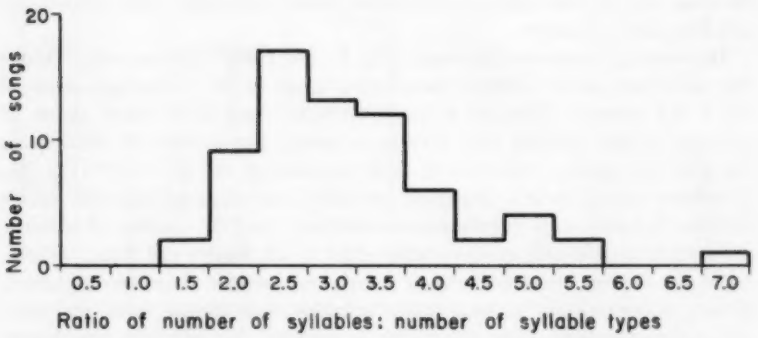


FIG. 3. Frequency distributions of maximum number of syllable repeats per song, and ratio of number of syllables to number of syllable types per song.

An estimate of the number of syllables which make up a trill can be obtained from the maximum number of consecutively repeated syllables in each song (Fig. 3). If we summarize the number of syllables in all of the trills in all songs the average number of syllables per trill is 4.1 ± 2.0, as compared with 1.7 ± 0.9 phrase syllables. The duration of syllables is similar in trills (0.138 ± 0.077 sec) and in phrases (0.135 ± 0.097 sec), the average figures for the songs as a whole being 0.137 ± 0.087 second. In phrases this duration is not related to the number of syllables present. In trills the two characteristics are correlated in an inverse fashion, the trills with most syllables having the shortest syllables. In those with two syllables, the average duration is 0.225 second per syllable; in those with three, 0.158 second; with four, 0.105 second; and so on, down to 0.050 second with

TABLE 2

SUMMARY OF DATA DISCUSSED COMPARATIVELY IN TEXT WITH ADDITION OF STANDARD ERRORS AND 95% CONFIDENCE INTERVALS*

	N	$\bar{X}$	s	$s_{\bar{x}}$	Confidence interval $p = 0.05$
Number of syllables per trill	139	4.1	± 2.0	± 0.17	± 0.33
Number of syllables per phrase	65	1.7	± 0.9	± 0.11	± 0.22
Trill syllable duration in seconds	138	0.138	± 0.077	± 0.0066	± 0.0129
Phrase syllable duration in seconds	111	0.135	± 0.097	± 0.0092	± 0.0182
Trill syllable duration in seconds by number of syllables per trill					
2-syllable trills	34	0.225	± 0.063	± 0.0108	± 0.0220
3-syllable trills	32	0.158	± 0.056	± 0.0098	± 0.0200
4-syllable trills	22	0.105	± 0.061	± 0.0130	± 0.0269
>4-syllable trills	446	0.085	± 0.033	± 0.0049	± 0.0100
Number of syllables per trill by position in song					
First trill	67	3.5	± 1.7	± 0.21	± 0.42
Other trills	72	4.6	± 2.2	± 0.26	± 0.52
Duration in seconds of trills by position in song					
First trill	67	0.67	± 0.16	± 0.020	± 0.040
Other trills	70	0.55	± 0.19	± 0.023	± 0.046
Duration in seconds of trill syllables by position in song					
First position	56	0.188	± 0.073	± 0.0097	± 0.0194
Second position	45	0.103	± 0.055	± 0.0082	± 0.0166
Third position	30	0.105	± 0.074	± 0.0135	± 0.0275
Fourth and Fifth positions	7	0.103	———	———	———
Note types by number of notes per syllable					
Vibrato notes	117	2.0	± 0.8	± 0.07	± 0.14
Non-vibrato notes	378	2.7	± 1.2	± 0.06	± 0.12
Number of notes per syllable					
Trill syllables	138	2.4	± 1.1	± 0.09	± 0.18
Phrase syllables	108	1.5	± 0.8	± 0.07	± 0.15

* N is the sample size; $\bar{X}$, the arithmetic mean; s, the standard deviation of the sample; and $S_{\bar{x}}$, the standard error of the mean. Symbols and calculations are based on Simpson, Roe, and Lewontin (1960).

eight syllables. The differences between two-, three-, and four-syllable trills are the only ones which are statistically significant (Table 2). The same relationship has been described in the trills of the Brown Towhee song (Marler and Isaac, 1960*b*).

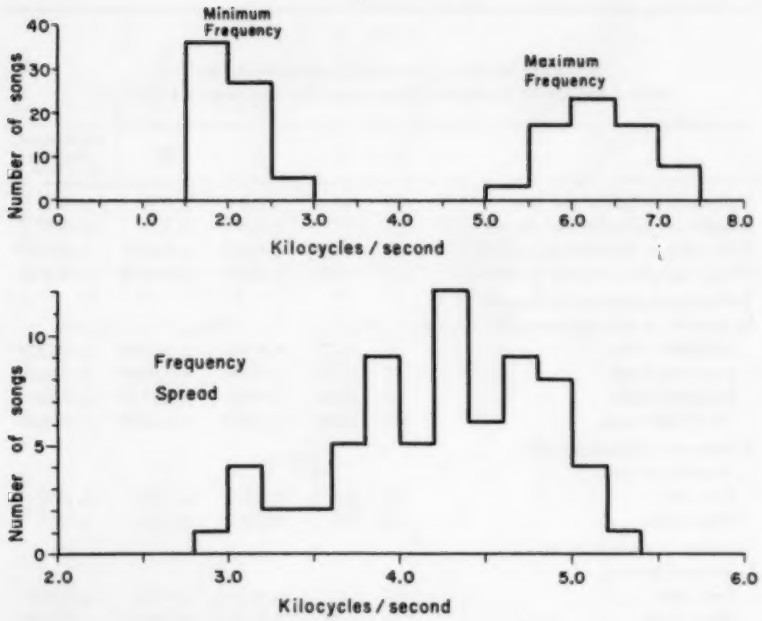


FIG. 4. Distributions of maximum and minimum frequencies per song, and frequency spread per song.

FREQUENCY CHARACTERISTICS

As in the songs of the Chipping Sparrow and the Brown Towhee, the frequency characteristics vary widely (Fig. 4). Once again, the minimum frequency (2.09 ± 0.25 kilocycles per second) is less variable than the maximum (6.39 ± 0.51 kc). The frequency spread which a song may span ranges from 3.0 to 5.4 kc (average 4.30 ± 0.58 kc).

TRENDS THROUGH THE SONG

Thus far we have established certain basic characteristics of Mexican Junco song; its duration, and the number of syllable types, the presence of phrases and of trills. Next we must look for any systematic changes in the course of the song. First, we could find no systematic changes in loudness through the song, as seen in amplitude displays of selected song patterns. In some cases the earlier syllables have the highest amplitude, in other cases, the loudest ones are later in the song. Within a trill the amplitude of the syllables is the same. The position of the trills in the song has already been

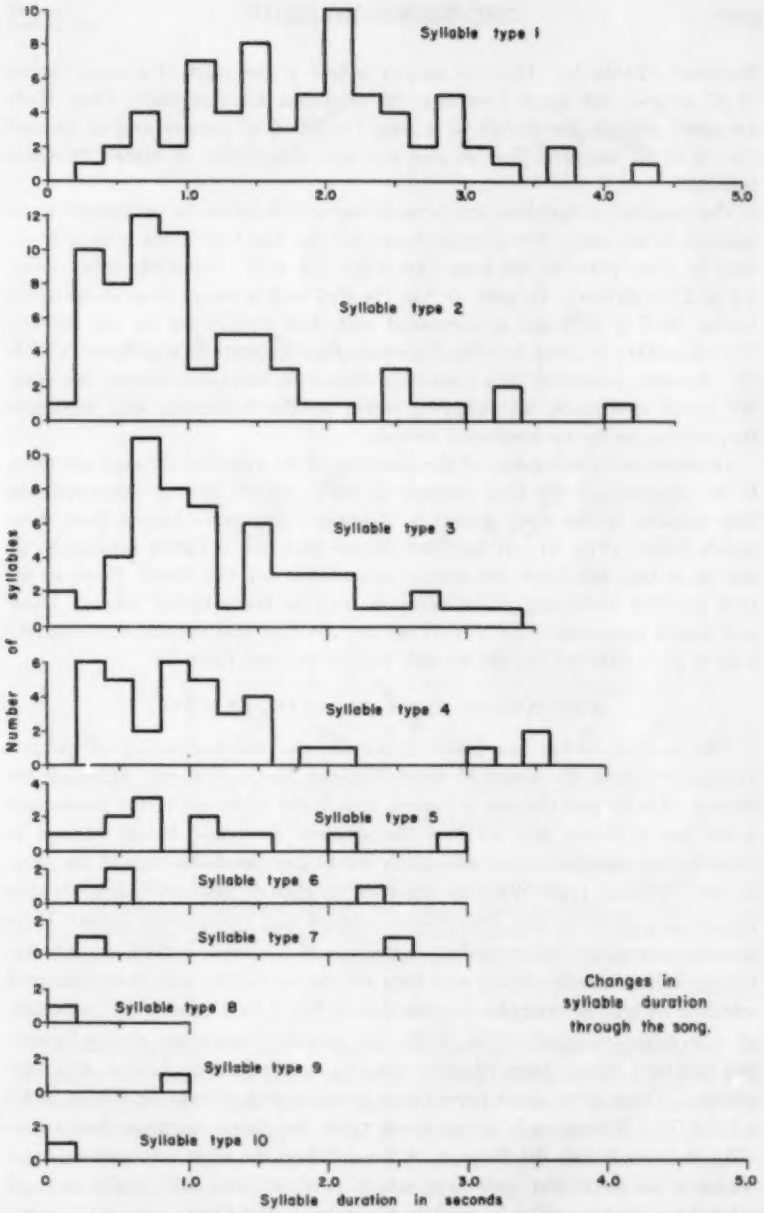


FIG. 5. Frequency distributions of changes in syllable duration by syllable type sequence through the song.

discussed (Table 1). There is usually a trill at the start of a song (in 56 of 67 songs), but apart from this the positions are irregular. Thus, there are often trills in the middle of a song (in 42 of 67 songs) and at the end (in 36 of 67 songs). The phrases are also distributed in rather irregular fashion.

The number of syllables which make up a trill seems to be related to its position in the song. The average figure for the first trill in the song is lower than in other parts of the song (1st trill: 3.5 ± 1.7 syllables; other trills: 4.6 ± 2.2 syllables). In spite of this, the first trill is longer than those which follow (0.67 ± 0.16 sec, as compared with 0.55 ± 0.19 sec for the others). The variability is great, but the differences are statistically significant (Table 2). Another possibility is a consistent change in frequency during the song. We could find none, by referring either to the maximum and minimum frequencies, or to the frequency spread.

Measures were also taken of the duration of the syllables through the song. If the duration of the first example of each syllable type is measured, the first syllable in the song proves to average consistently longer than those which follow (Fig. 5). If we treat phrase and trill syllables separately we can show that the latter are mainly responsible for this trend, those in the first position averaging about twice as long as those in the second, third, and fourth positions (0.19 ± 0.07 sec for the first trill syllable as compared with 0.10 ± 0.06 sec for the second, and so on; see Table 2).

STRUCTURE OF SINGLE SYLLABLES AND NOTES

The analysis so far has failed to account for the impression of extreme variability which the songs of these Mexican Juncos convey. Although the pattern of trills and phrases is varied, it is in the structure of the component notes and syllables that we find the greatest diversity. In an attempt to describe this structure more adequately we took separate tracings of the notes in each syllable type. Various attempts to classify the 497 notes resulted finally in a division into two classes, vibrato and non-vibrato notes. These in turn were subdivided according to the type of frequency inflection: whether rising, falling, steady, rising and then falling, or falling and then rising. A selection of typical examples is presented in Fig. 6 to illustrate the variability of note structure. Only eight of the ten possible classes are shown because two did not occur (non-vibrato: steady; and vibrato: falling and then rising). There were about three times as many non-vibrato as vibrato notes (378:117). Within each group some types are more common than others (Fig. 6, legend) but the diversity is nevertheless the most impressive aspect. There is no particular note type which predominates sufficiently over all other types that it could be said to characterize the song.

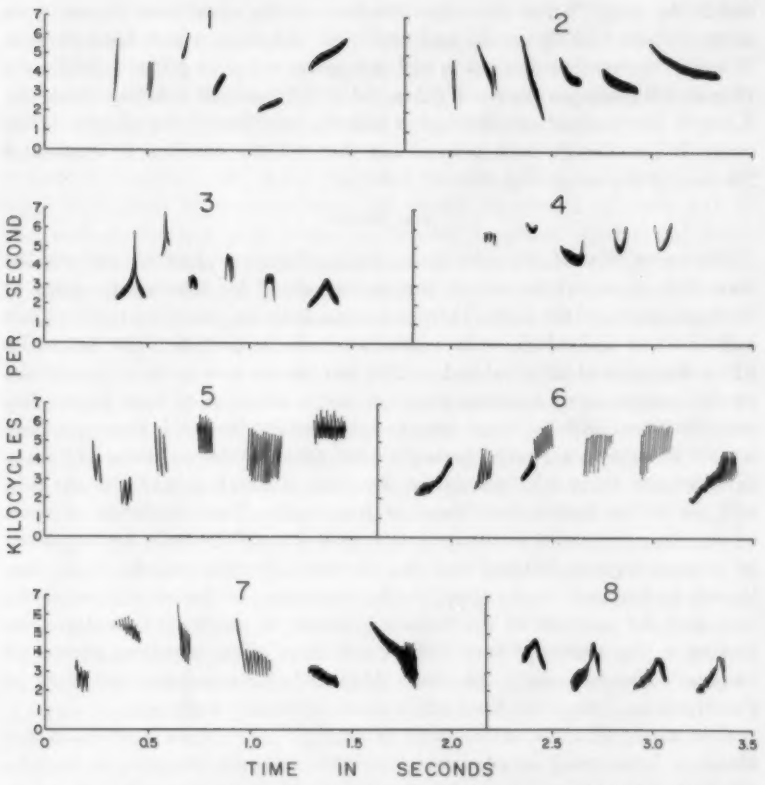


FIG. 6. Note types selected from various songs: The percentage which each note type contributes to the total is given in parentheses. 1 to 4—non-vibrato: (1) upward inflected (17.9), (2) downward inflected (25.2), (3) upward then downward inflected (26.2), (4) downward then upward inflected (6.8). 5 to 8—vibrato: (5) not inflected (10.3), (6) upward inflected (5.2), (7) downward inflected (7.6), (8) upward then downward inflected (0.8).

We also examined the way in which notes are organized into syllables. By recording the number of notes per syllable from which each individual note of the sample had been drawn, we found that vibrato notes come from syllables with fewer notes (2.0 ± 0.8 per syllable) than the non-vibrato notes (2.7 ± 1.2 per syllable, a significant difference; Table 2). Apart from this, each note type is equally likely to occur in a long syllable as in a shorter one. All types are also equally likely to occur at the beginning, middle, or

end of the song. Nor is there any difference in the occurrence of note types in the syllables which are formed into trills and those which form phrases. However, the number of notes in trill and phrase syllables differs significantly (1.5 ± 0.8 notes per phrase syllable, 2.4 ± 1.1 per trill syllable; Table 2). There is also a separate relationship with the position of the syllable in the song. It has already been pointed out that syllable duration is greatest at the start of the song (Fig. 6).

DISCUSSION

The variability of Mexican Junco song.—Detailed physical analysis has done little to dispel the initial impression gained by listening to songs of Mexican Juncos in the field. There is a remarkable degree of variability from individual to individual, even within a single population. The properties which the songs of all individuals within this sample tend to have in common, on the average, are: a certain duration, and a selection of from two to five syllable types, with at least two and sometimes three of these repeated several times to form trills, giving a total of about ten syllables per song. Syllables are about 0.14 seconds in duration, although syllables in the first trill are rather longer than those in later trills. The variability of some of the other properties of the song is very striking. The trills are organized in a more regular fashion than the phrases. Nevertheless, the trills may appear in any part of the song, at the beginning, in the middle, or at the end, and the position of the loudest syllables is similarly irregular. The frequency characteristics vary widely, and there is no consistent pattern of frequency change through the song. Above all, there is great variability in the structure of the notes from which the syllables are built up.

Compared with some of the other emberizine finches, there is no doubt that Mexican Junco song is excessively variable in some respects, at least in this part of the range. The variability is probably less extreme than in songs of some of the more versatile singers, such as certain thrushes. Few quantitative studies of variation in bird song have yet been made, so that precise comparisons are difficult. Detailed syllable structure has proved to be variable in several species such as the Rufous-sided Towhee, *Pipilo erythropthalmos* (Borror, 1959*a*), the Brown Towhee, *Pipilo fuscus* (Marler and Isaac, 1960*b*), and the Chipping Sparrow, *Spizella passerina* (Borror, 1959*b*; Marler and Isaac, 1960*a*), and it may be that the Mexican Junco is a typical emberizine in this respect. The much simpler song of the Oregon Junco (*Junco oreganus*) is also variable in syllable structure, even though there is usually only one syllable type per song (Marler, Kreith, and Tamura, in press). Frequency characteristics have proved to be similarly variable in other species.

The variability of the over-all pattern in time is more unusual. The Rufous-sided Towhee has a similar variety of syllable types in each song, but they

are arranged in a fairly regular pattern, so that Borror (1959*a*) can speak of an introduction and a trill. The European Chaffinch also has a variety of syllable types in each song, but they are organized into a series of trills, and an end-phrase (Marler, 1952; Thorpe, 1958). There is no such regularity in the way in which trills and phrases are placed in the songs of Mexican Juncos.

Song recognition.—We have suggested elsewhere that variability in bird songs is unlikely to be accidental, but should be related in some way to the function which a song performs (Marler, in press; Marler and Isaac, 1960*b*). It has been argued that specific and individual recognition, both of which can be mediated by bird songs, will encourage different evolutionary trends, toward stereotyped species-specificity in certain characters, and toward individual variability in others. It is thus of some interest to determine which song characters are shared by all members of a population, and which differ from individual to individual. As we have seen, Mexican Junco songs have many characters which vary consistently from individual to individual, and relatively few which are shared by all members of the population. Moreover, those which are shared are rather vague and indefinite in nature, so that we can only characterize the species-specific qualities of the song in an approximate way. We are thus led to ask what qualities are used by the juncos themselves in specific recognition. A final answer can only be given to this question by experiments, which would have to take into account the songs of other birds in the area, with which there might be confusion. The avifauna in the pine woods around El Salto is a simple one, occupying extensive uniform areas. The small number of bird species present may be a factor in determining the lack of highly stereotyped species-specific characters in junco song. This appears to be the case on some small islands, where an increased variability of songs as compared with the mainland populations can sometimes be correlated with the reduced avifauna, which simplifies the problem of specific song recognition (Marler, 1960).

There is an abundance of characters to permit individual recognition by song, even for a human observer. It would be interesting to know the developmental basis of these individual characteristics. Juncos living together in a group sometimes shared resemblances in syllable structure which could have a learned basis or a genetic one. The study of song development in captive-raised birds, which we plan to make in the future, will help us to decide between these two alternatives.

SUMMARY

The songs of 63 male Mexican Juncos living together in the same population, in Durango, Mexico, proved to be very variable in many characteristics. The average duration is 1.63 $\pm$ 0.29 seconds. The number of syllable types per song pattern usually

ranges from two to five. Syllables average 0.137 ± 0.087 second in duration, with the first in the song tending to be longer than those which follow. Some syllables are given singly, others are repeated in trills. The position of the trilled parts of the song, of which there are usually two, sometimes one or three, is very variable. The average number of syllables per song is 10.1 ± 2.9. Most of these occur in the trills which make up the greater proportion of the song, and are the most regular component. The frequency characteristics vary widely. There are no systematic changes in loudness or in tempo through the song, except for a tendency for the first trill in the song to have fewer, longer syllables than those which follow. The individual notes from which the syllables are built up have a wide variety of forms. The species-specific qualities of the songs of this population of Mexican Juncos are less definite and stereotyped than in some other emberizine finches.

ACKNOWLEDGMENTS

The expedition to Mexico, on which the songs were recorded, was made possible by a grant from the Associates in Tropical Biogeography, for which we are most grateful. We are indebted to Mrs. Emily Reid, who spent a great deal of time and trouble preparing the figures, and to Mr. W. R. Fish for helpful criticism. And, finally, thanks are due to the National Science Foundation for a research grant, under the auspices of which this work was carried out.

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DEPARTMENT OF ZOOLOGY, UNIVERSITY OF CALIFORNIA, BERKELEY, 21 MARCH 1960

GENERAL NOTES

Dermestids killed when feeding on skeletons of birds killed by organic insecticides.—During the summer of 1959, the Cooperative Wildlife Research Unit at the University of Massachusetts conducted studies on the toxicity of certain organic insecticides using the American Woodcock (*Philohela minor*) as an experimental animal. The insecticides were carefully weighed doses enclosed in gelatin capsules and force-fed individually to birds of known sex, age, and weight. Some of the birds which died were presented to me for the purpose of preparing skeletal specimens to add to our collections. Two birds were roughed out, dried, and placed in separate boxes on clean cotton in the bottom of a five-gallon aquarium which had been used previously for this same purpose, become dirty, and been cleaned with plain hot tap water. A number of adult and older larval stages of the dermestid, *Dermestes maculatus* Deg. (= *D. vulpinus* Fab.), were removed from an active colony and placed on the specimens. The next day most of the beetles were dead. Some were kicking feebly and a few were still able to move about. Every one was dead by the third day. One of the woodcock skeletons was then soaked for two days in several changes of hot water, dried, and beetles placed on it with the same results. Infestation by mites as a cause of the death of the dermestids was clearly ruled out. The insecticide and dosages resulting in the death of these two woodcock were: woodcock No. 12, five doses of Dieldrin (each dose 1.25 mg/kg at daily intervals), and No. 24, a single dose of Dieldrin at 25 mg/kg (killed the bird within three hours after administration).

During the early fall I was called to the home of a friend to receive a sick second-year Herring Gull. As I was holding the gull while talking to Mr. Chisholm, the bird extended its neck slowly and died without a tremor. The symptoms were not at all similar to those of DDT poisoning and, since Mr. Chisholm had mentioned that the bird had some slight respiratory difficulty, I was guessing it had died of aspergillosis. About a month later, I removed the bird from the freezer, roughed it out, and placed it in a box on clean cotton in a five-gallon aquarium with some dermestids. On the following day the majority of the beetles were dead or dying and subsequently every beetle was killed. I do not know whether the aquarium was the same one used for the woodcock. Even if it were, the chances of contamination would appear to be slight, since the cotton was clean, the aquarium used for the woodcock had been thoroughly washed with soap and water and rinsed a number of times, and most of the beetles appeared to remain in the cardboard box containing the skeleton. A quick check in our collection reveals one Robin skeleton which had been brought in with convulsive tremors characteristic of DDT poisoning. This apparently had had no appreciable effect on the dermestids.

The results of these experiences suggest that birds which are found dead or dying should not be placed in vigorous, active colonies of dermestids. They also suggest that, with proper experimental data for background, the dermestid might prove useful in determining whether a bird had died from ingesting lethal quantities of certain organic insecticides. I would like to thank the Wildlife Unit and Mr. Wendell Dodge for providing the specimens and data on the woodcock, and Dr. Marion E. Smith for identification of the dermestids.—L. M. Bartlett, *Department of Zoology, University of Massachusetts, Amherst, Massachusetts, 24 March 1960.*

Some shorebird records from Mexico.—Among our more interesting observations while in Mexico were those of shorebirds, a group with which Mrs. Coffey and I have spent quite some time. Most species we observed, chiefly of interest as transients, are

being reported elsewhere while data on five are given here. Except where noted, all localities are in Veracruz. A favored strip of pits was along the Tampico-Valles highway, starting at Kilometer Post 9, almost to the village of Cacalilao at Km. 33, on the first rise, all in the state of Veracruz. At Km. 17.7 a side road runs south along Laguna Chila (almost dry on recent spring visits).

The Mexican Check-list (Pt. I, Friedmann, Griscom, Moore, 1950. *Pac. Coast Avif.*, 29:91) does not indicate records of the Semipalmated Plover (*Charadrius semipalmatus*) for the state of Veracruz. However, Frederick W. Loetscher, Jr. (1955. *Auk*, 72:26) gives a number of records for the state while Dean Amadon and Don R. Eckelberry (1955. *Condor*, 57:67) found the species, 3 May 1952, at the Bay of Alvarado. Our reports are: Tecolutla, two on 7 December 1949; east of Cacalilao, one on 21 November 1956; the beach, Coatzacoalcos, 50 on 3 December 1956, and on 4 December, eleven there and five near Nanchital. Apparent first reports for Guerrero are ours from near Acapulco; 17 at Pie de la Cuesta, 26 November 1956, and three at Colonia Copacabana, south of Puerto Marqués, the next day.

We know of no previous nesting record of the Snowy Plover (*Charadrius alexandrinus*) from the east coast and, except for Yucatán, but one previous report of the species on this coast. This latter was the four listed for the Tampico Count by L. Irby Davis, et al., 1–2 January 1953 (Edgar Kincaid, Texas Orni. Soc. Newsletter I (11), 9 December 1953). These may have been in Veracruz rather than Tamaulipas. On 4 December 1956, two singles were seen at Coatzacoalcos. Our other records are east of Cacalilao: the pit at Km. 9, and Laguna Chila. On 28 May 1955, two at Km. 9 gave indications of nesting but no nest could be found then or the next day when four were present. Along Laguna Chila on the 29th we saw one, two, and four and found a nest with four eggs which we photographed, along with that of a Black-necked Stilt. The Km. 9 pit was flooded by rain, overnight, and no shorebirds were left there, 30 May. On 31 May 1957, we found two pairs at Km. 9 and four, possibly nesting, at Laguna Chila (one-third dried up).

For the Wilson's Plover (*Charadrius wilsonia*), the Check-list gives only Veracruz (two records) and Yucatán on the east coast. Site of one listed Veracruz specimen is east of Cacalilao where we saw three singles on 11 May 1954, ten on 28 and 29 May 1955, and 20 to 23 (three spots) on 31 May 1957, and 20 April 1958. The 1955 birds acted as if nesting, but the birds were gone 30 May after the water level rose from rain. Amadon and Eckelberry (1955. op. cit.) found this species at the Bay of Alvarado, and Loetscher (1955. op. cit.) found it common at the city of Veracruz.

Sanderling (*Crocethia alba*). Guerrero is omitted under this species in the Check-list. However, Wm. B. Davis (1944. *Condor*, 46:10) reports two collected 14 August 1942, at Laguna Coyuca (near Acapulco) and that the species were "numerous" there. We saw only seven, all at the Colonia Copacabana beach, 27 November 1956.

The Willet (*Catoptrophorus semipalmatus*) was seen but a few times: 7 December 1949, one, south of Tecolutla, and 2 December 1956, ten near Veracruz. East of Cacalilao, we saw one, 29 and 30 May 1955, two singles and a pair on 21 November 1956, and 32 on 20 April 1958.

Another shorebird not credited to Guerrero by the Mexican Check-list is the Black-necked Stilt (*Himantopus mexicanus*). On 25 November 1956, I found two at a small lake north of Chilpancingo and five just southeast of Acapulco. The next day we saw a total of 72 widely scattered between Pie de la Cuesta and the Río Atoyac; then, on the 27th we counted 21 between Puerto Marqués and the new airport for Acapulco.—Ben B. Coffey, Jr., *672 N. Belvedere, Memphis 7, Tennessee, 21 March 1960.*

A Hybrid between the Painted and Varied Buntings.—Following the death in 1945 of the veteran collector, H. H. Kimball, the late Max M. Peet purchased his residual collection, numbering 15,146 bird skins and numerous sets of eggs. Through the generosity of Mrs. Peet, Dr. Peet's collection was donated to the University of Michigan Museum of Zoology. Unfortunately, most of the Kimball birds bear labels with only the sex and date of collection. We do know that he moved from Reserve, Catron County, New Mexico, to Cameron County, Texas, between 25 March and 18 April 1930, and resided in southern Texas through 1944.

Among the birds Kimball collected in southern Texas is an adult male bunting which appears to be a hybrid between the Painted Bunting (*Passerina ciris*) and the Varied Bunting (*P. versicolor*). The bird was taken 9 June 1934, presumably near Los Fresnos, Cameron County, where Kimball lived at the time. (We have another specimen collected on the same date with "Los Fresnos" in Kimball's writing on the label.)

Compared with two adult male Painted Buntings and four adult male Varied Buntings taken in June in Cameron County, the presumed hybrid is more like the Painted Buntings in pattern and general appearance. The underparts are red as in the Painted, but somewhat paler and duller. The top and sides of the head are solid blue as in the Painted, but the color is lighter (near Light Blue-Violet of Ridgway, 1912, Color Standards and Color Nomenclature), but not so pale as the forehead of the Varied. The back is a duller, bluer green than in the Painted (the two tones present being near Peacock Green and Meadow Green of Ridgway) and lacks the golden tones of that species. The green extends less far posteriorly than in the Painted, resembling in extent the mantle of the Varied. The lower back, rump, and upper tail coverts are intermediate in color between the rose-red of the Painted and the blue of the Varied, being between Light Violet and Hortense Violet of Ridgway. The rectrices are also intermediate in color between those of the presumed parental species, being paler and less blue (more violet) than in the Varied. The primary edgings are bluish as in the Varied Bunting, but one left "tertial" has a broad dull green outer web as in the Painted but of a darker and bluer green.

The wing length (chord) of 25 adult male Painted Buntings from southern Texas varies from 68.5 to 74.0 mm (mean, 71.3). Four adult male Varied Buntings from the same area have wing lengths of 65.5, 66.0, 67.0, and 68.0 mm (mean, 66.6). The wing of the hybrid measures 69.0 mm and is thus within the expected range of variation for the southern Texas populations of both species. It is, however, almost exactly intermediate between the means for my two samples. (These populations of the two species do not differ significantly in tail length, and the hybrid, with a tail length of 55.5 mm, agrees with both.)

The Indigo and Lazuli Buntings (*Passerina cyanea* and *P. amoena*) hybridize over a wide area in the Great Plains (Sibley and Short, 1959. *Auk*, 76:443–463). Although the Painted and Varied Buntings are probably less closely related, hybridization between them in southern Texas, where their breeding ranges overlap, is not surprising.—Robert W. Storer, *University of Michigan Museum of Zoology, Ann Arbor, Michigan, 31 March 1960.*

Recent brood records for the White-winged Scoter in North Dakota.—White-winged Scoters (*Melanitta deglandi*) were once considered to be locally common as breeders in parts of North Dakota, especially in the Devils Lake region (H. K. Job, 1898. *Osprey*, 3:39; 1899. *Auk*, 16:161–165; 1902. Among the water-fowl, pp. 189–190, Doubleday, Page and Co., New York, N.Y.; A. C. Bent, 1951. Life histories of North American wildfowl [reprint edition], Vol. II, pp. 132–133, Dover Publications, Inc., New York, N.Y.). These observations constituted the most southerly breeding records for the species in North America.

According to my review of the literature, White-winged Scoters became rare as breeding birds in North Dakota between 1900 and 1920. After the observations of Job and Bent, mentioned above, no breeding record is available until 1917, when F. M. Bailey observed half-grown young at Sweetwater Lake, Ramsey County, in late August (original paper not seen; quoted by N. A. Wood, 1923. A preliminary survey of the bird life of North Dakota, pp. 20–21, Misc. Publ. No. 10, Univ. of Mich., Ann Arbor). Wood observed a nest with 12 well-incubated eggs at Stump Lake, Nelson County, on 25 July 1920.

F. W. Cook (1946. *Auk*, 63:251–253) summarized the summer occurrence of White-winged Scoters on National Wildlife Refuges in the north-central United States. Adult birds were recorded on two North Dakota refuges in the summers of 1938, 1940, and 1941. This paper reported the next evidence of breeding by scoters in North Dakota: on 28 July 1936, Seth Low found two White-winged Scoter broods, each containing nine juveniles, on a lake five miles south of Denbigh, McHenry County.

Following this observation no brood records were obtained until 1952, when a female with a brood of nine young was seen at Des Lacs Refuge, Burke County, by Refuge Manager H. Huenecke (1952. *Audubon Field Notes*, 6:287). In 1953, a female with a brood of four young was observed in the same vicinity by Refuge Manager K. D. Dybsetter (1953. *Audubon Field Notes*, 7:314).

On 15 August 1955, while observing waterfowl at the Lostwood National Wildlife Refuge in Burke County, North Dakota, I saw a female White-winged Scoter with a brood of eight ducklings. The ducklings appeared to be about one week old. During a previous visit to this refuge (12 July 1955), I saw two pairs of White-winged Scoters in this same area, a pothole known locally as Knutson's Slough. The female and brood were observed within 100 yards of where the pairs were seen on 12 July.—H. F. Duebbert, *North Dakota Game and Fish Department, Oakes, N. D., 28 March 1960.*

Marsh Hawk and Common Crows feeding simultaneously on roadside-carrion.—At 6:45 AM, shortly after daybreak, on 7 March 1960, one mile north of Lone Elm, Anderson County, Kansas, I observed an adult male Marsh Hawk (*Circus cyaneus*) and three Common Crows (*Corvus brachyrhynchos*) simultaneously feeding on a freshly killed Eastern Cottontail (*Sylvilagus floridanus*). The carcass was lying in the west lane of a hard-surfaced road, and I presumed that the rabbit had been struck and killed by an automobile. All four birds were frightened away from the immediate area by approaching cars, and none returned during the short time that I was examining the eviscerated and well-mutilated rabbit (probably an adult). Crows are commonly observed feeding on roadside-carrion. The Marsh Hawk has also been said (Fisher, 1893. The Hawks and Owls, etc., U.S. Dept. Agric., Division of Ornithology and Mammalogy, Bulletin No. 3) to feed on carrion "when hard pressed." Bent states (1937. Life Histories of North American Birds of Prey, *U.S. Natl. Mus. Bull.* No. 167) that the Marsh Hawk willingly partakes of carrion. Errington and Breckenridge (1936. Food Habits of Marsh Hawks, *Amer. Mid. Nat.*, 17:847) and Randall (1940. Seasonal Food Habits of the Marsh Hawk in Pennsylvania, *Wilson Bull.*, 52:170) have reported that the Marsh Hawk feeds on roadside-carrion. Otherwise, I have found no specific examples on record of the Marsh Hawk feeding on carrion, with the exception of game birds freshly killed by hunters (see Fisher, op. cit.), which birds are carrion in a broad sense of the word. To my knowledge, the Marsh Hawk has never been reported to feed simultaneously with crows. The hawk's feeding on the rabbit and the feeding together of the two species of birds may have resulted from intensified hunger, perhaps effected by recent and severe snowstorms in eastern Kansas.—Charles A. Long, *Museum of Natural History, University of Kansas, Lawrence, 18 March 1960.*

Two observations on the orientation of day migrants heading inland from the Massachusetts coastline.—(1) On 22 September 1959, between 0715 and 1000 (EDT), while driving in a semi-circle around the coast of Cape Cod Bay from Wellfleet Bay past Plymouth to Lincoln, I kept a count of the Blue Jays (*Cyanocitta cristata*) crossing the highway, and estimated their direction by comparing it with the direction of the sun at the time. The observations were nearly continuous except for occasional periods of watching the road and traffic.

From 0715 until about 0800, while still on the Cape (southwest wind, 10 mph), I saw 12 Blue Jays flying singly, heading in directions that lay between south and southeast by south. Between the Cape Cod Canal and Lincoln (light west wind) I saw 36 jays in all, heading in directions varying from southwest by west to west. As soon as I crossed the Cape Cod Canal I saw birds oriented west, and the last group of six birds I saw near Lincoln was headed southwest. I saw four jays headed northeast, between Plymouth and Route 128, and two groups (one of two and one of three) flying northeast, near Lincoln. The directions were accurate to within 10 or 15 degrees, and show that the birds were following different average directions. The birds on the south and east sides of Cape Cod Bay were flying south; those on the west side of the Bay were flying west; those near Lincoln were flying southwest.

If we plot these directions on a map of Cape Cod Bay region, it appears that the Blue Jays near the coast were flying in many directions, but in each case directly away from the water; while those farther inland were taking a single, generally southwest, direction. If the birds on the Cape were merely leaving the coast, they cannot have been aware of the presence of the coast farther south.

(2) On Plum Island on 9 October 1959, a group from the Hatheway School of Conservation and I saw the southward migration of five flocks of Double-crested Cormorants (*Phalacrocorax auritus*) between 1030 and 1300. These flocks numbered between 20 and 45 birds. They were all headed in a direction just west of south, which led them to the coastline. One flock passed over Newburyport Harbor; three others met the coast near the mouth of the Merrimack, and a fourth met the coast near Plum Island Point.

We watched three cormorant flocks come in from over the sea in a regular formation with steady flight, toward the shore, from a point east of the Isles of Shoals, New Hampshire, until they started to pass over the beach. At this point the three flocks broke formation, but the two flocks that we saw near Newburyport Harbor quickly re-formed their V and followed the coastline. The flock of about 45 birds that we saw cross the coast at the southern end of Plum Island broke up and started to circle higher and higher. After the whole group had circled twice, a section of about 15 birds turned from the rest, formed a loose V and moved across the beach in a southwest direction which would carry them inland of Cape Ann. They then shifted their course to the south and continued in a south by west direction out of sight over the land. The larger group continued to circle higher, and was blown gradually offshore by a gentle northwest wind for a period of about 10 minutes until they were at about 3,000 to 5,000 feet up; then they also formed a loose flock and moved to the southwest. They turned again and followed the shore in a southerly direction over Ipswich Bay, but continued on in this southerly direction to pass overland west of Cape Ann.

The cormorants were following a consistent heading across the sea, and as they met the shore, they altered their course as Geyer has suggested for his *Leitlinien* (leading or deflecting lines) (1929. *J. f. Ornith.*, 77:17–32), and the fact that deflection and "indecision" were involved is shown by their milling about.

This course, and these actions, compared with the coastline of New England, and the

migration route of Double-crested Cormorants shown in the map in an article by Baird and Nisbet (1959. *Mass. Audubon*, May–June), show that a southwest direction is the primary one for cormorants coming from Maine to cross Massachusetts into Narragansett Bay and Long Island Sound.

On both days on which these diurnal migrations of jays and cormorants were seen, the weather was clear and there was a light wind, southwest and west on 22 September and northwest on 9 October. On both days there was little other evidence of migration, and both days followed several days unsuitable for migration. These two observations point to the compromise between the primary direction and the effect of topography, in the migration of New England birds. These observations show the influence of these deflecting lines, which have led most American students of migration since William Brewster to consider use of topographic features as the primary orientation mechanism in bird migration. Many observations are needed to clarify how diurnal migrants make their way along the New England coast, but at present it is reasonable to accept these observations as further evidence that they use sun orientation together with clues from topography to maintain their primary directions and avoid local dangers.—WILLIAM H. DRURY, JR., *Drumlin Farm, South Lincoln, Massachusetts. Contribution Number HS-30 from the Hatheway School of Conservation, 25 April 1960.*

Phoebe builds over dead young.—While banding nestlings in the summer of 1959 I observed an unusual nesting of the Eastern Phoebe (*Sayornis phoebe*) about five miles from State College, Pennsylvania. The nest was located just above eye level on a ledge of a rock cliff. When first discovered on 29 May two well-feathered young could be seen—one a Brown-headed Cowbird (*Molothrus ater*) and the other a phoebe. The young were not disturbed. The nest was next visited on 1 June at which time it contained a few loose bits of moss on top of two dead young. Since these two dead young were at an earlier stage of development than those previously observed they must have been hidden beneath the cowbird and phoebe at the time of the earlier visit on 29 May. The adult phoebes were protesting quite near so I decided to check again at a later date. By 8 June about an inch of fresh moss and lining material had been deposited on top of the dead young in the nest, and four eggs had been laid. On 18 June only three eggs could be seen, and on 30 June the nest was empty. The adult phoebes were still in the area on 30 June but showed no interest when I approached the nest. The nest was later collected and examination verified the presence of the two dead young beneath the added layer of nest material.—DOROTHY L. BORDNER, *926 West Beaver Avenue, State College, Pennsylvania, 12 July 1960.*

A prehistoric record of the Trumpeter Swan from central Pennsylvania.—Sections of the Sheep Rock Site, an Indian rockshelter located approximately 22 miles south of Huntingdon, Huntingdon County, Pennsylvania, were excavated during the summers of 1958 and 1959. Preliminary test pits dug in 1958 revealed quantities of dry organic material such as cordage, fabric, and wood as well as the usual amounts of flint projectile points and chips, bone remains, and other Indian refuse typical of such dry rockshelter sites. The Sheep Rock Site is dated at approximately 1500 A.D. Under the sponsorship of the Pennsylvania Historical and Museum Commission, Harrisburg, more detailed excavations were undertaken for an eight-week period in 1959 and they were directed by John Witthoft and W. Fred Kinsey III, Curator of Anthropology, Pennsylvania State Museum.

The presence of corn and beans in the midden deposits suggests that agriculture was practiced by some of the later groups occupying this site. However, the quantity of vertebrate remains throughout all excavated levels points to the significance of the local fauna

as probably the principal source of food for these people. In addition to the large number of bone fragments, which have not yet been completely analyzed, numerous bone artifacts were also encountered. Although several are of particular archaeological interest, the worked ulna and humerus sections of a swan are the most significant from a zoological point of view.

The proximal half of a left ulna and a right humerus of the Trumpeter Swan (*Olor buccinator*) were found in association with materials from these dry middens. Both wing bones were cut off almost exactly at the mid-point of the shaft, and the cut ends then had been beveled inwardly. Possibly these tools (?) were used as some type of gouge or perhaps they served as handles; their polished appearance suggests considerable handling. The ulna was sent to me first by Mr. John E. Guilday, Assistant Curator of Comparative Anatomy, Carnegie Museum, Pittsburgh, and was tentatively identified as *O. buccinator*. Since the locality is considerably out of this swan's known range, it was sent to Dr. Alexander Wetmore, Research Associate, Smithsonian Institution, Washington, who stated (letter of 18/11/59) that "the swan ulna is a good specimen of the Trumpeter Swan of large size." In scraping (or cleaning?) the ulna, the outer edge of the external and internal cotyla, the tip of the olecranon, and a small area immediately posterior to the olecranon on the anconal surface, were removed. The edge of the deltoid crest, internal tuberosity, pneumatic fossa, and bicipital crest of the humerus were also scraped and/or broken away.

The diameter (breadth) of the ulna shaft at the point where it was cut is slightly larger (14 mm. vs. 13 mm.) than the largest adult Trumpeter Swan ulna in the Illinois State Museum collection. In contrast, the breadth of the humerus measured at this point is approximately 1 mm. less (17 mm. vs. 18 mm.) than the humerus of this same swan, thus suggesting the probability that two individuals are represented. Extremely close similarities of anatomical features between the Trumpeter Swan and the Whistling Swan (*Olor columbianus*) often make specific determinations questionable; although this cut humerus is slightly greater in proportion to the largest adult Whistling Swan specimen in the Illinois State Museum collection, it may possibly represent a very large individual of *O. columbianus*.

Apparently there are no authenticated records of the Trumpeter Swan for Pennsylvania, and Indiana is given as the eastern edge of its former breeding range in the fifth (1957) edition of the A.O.U. Check-list of North American Birds (p. 58). Todd (1940. Birds of Western Pennsylvania, p. 67) states that "The Trumpeter Swan (*Cygnus buccinator*) is another species which may have occurred formerly but for which the evidence of occurrence is likewise unsatisfactory." There is one possible record as suggested by Sutton (1928. *Annals Carnegie Mus.*, 18(1):19–239): "Mr. William Foust of Conneaut Lake is said by Mr. Welshons to have taken a Trumpeter Swan at the Lake in November, 1909." Remains of this swan have been reported from Ohio (R. M. Goslin, 1955. *Ohio Jour. Sci.*, 55(6):358–362) and have been found commonly at certain sites in Illinois (P. W. Parmalee, 1958. *Auk*, 75(2):169–176). It is reasonable to assume, therefore, that when this species inhabited eastern North America, occasional migrating or wandering flocks may have occurred in Pennsylvania. This one record (ulna and possibly the humerus) points to the prehistoric occurrence of the Trumpeter Swan in central Pennsylvania; with the excavation of addition faunal materials from various sites and the probable recovery of other swan material, the former occurrence of this species may be definitely established for the state.—Paul W. Parmalee, *Illinois State Museum, Springfield, Illinois, 18 December 1959.*

Food competition among closely related sympatric species.—From this viewpoint, the following incident may be of interest. Late in the afternoon of 6 June 1959, a Yellow-billed Cuckoo (*Coccyzus americanus*) and a Black-billed Cuckoo (*Coccyzus erythropthalmus*) were observed feeding on some spiny black caterpillars, about one and a half inches long, which were clustered on many tips of the branches all over a willow tree standing beside a sluggish stream. Both cuckoos used the same techniques. Sometimes they would hop to a branch favorably located below a cluster of caterpillars and then fly up to the cluster, fluttering rather awkwardly until one was captured. At other times they would work out along a limb until a caterpillar could be reached by stretching. In any case, the prey was vigorously worked through the bill from one end to the other several times before swallowing. It seemed that the Black-billed Cuckoo prepared its food more thoroughly than the Yellow-billed. Four instances of conflict were observed; in every case, the Black-billed was the aggressor and the Yellow-billed retreated without resistance to another part of the tree. The Black-billed sang twice, the Yellow-billed was silent throughout. The Black-billed captured 11 caterpillars in an hour and a half, of which nine were eaten in the tree and two were carried off. The Yellow-billed was seen to eat six and, so far as could be determined, never left the tree during the observation period. At least an equal number of caterpillars were dislodged from the tree since the wing-fluttering technique frequently shook loose two or three caterpillars in addition to the one taken. At 9 AM the following morning, a careful examination failed to disclose a single caterpillar. Although it cannot be proven, it seems to be a fair assumption that the cuckoos completed the job during the early hours of the morning, because the only other species present here in June which might have participated, Blue Jays (*Cyanocitta cristata*) and Scarlet Tanagers (*Piranga olivacea*), were not observed in the immediate vicinity during this time. Thus, in interspecific competition, a Black-billed Cuckoo dominated a Yellow-billed Cuckoo where an abundant food supply existed, but the competition did not really interfere with the food supply of the dominated species.—R. O. BENDER, *Cobb's Mill Road, R. D. No. 1, Bridgeton, New Jersey, 6 January 1960.*

LETTER TO THE EDITOR

Further Comments on Variation in Vireo

I would like to take this opportunity to clarify certain misunderstandings which, as A. L. Rand (1961. *Wilson Bull.*, 73: 46–56) points out, seem to have resulted from my paper on "Adaptive variation in the genus *Vireo*" (1958. *Wilson Bull.*, 70: 307–346).

(1) In my paper, I was attempting to show that the effects of selection pressures for large size in the cooler parts of the ranges of species are frequently masked in other regions by additional selection pressures superimposed on the operation of the effect of low temperature. Taking Bergmann's rule for granted, I concentrated on additional factors which conceivably might effect geographical variation in body size and wing length. To make sure that this would not be misunderstood, I introduced my paper with these sentences (1958: 308): "Before continuing, I would like to point out that my conclusions, reported in this paper, on the adaptive significance of variation in body size within the species of *Vireo* and some other New World species *do not invalidate* Bergmann's rule. Rather, I interpret my findings to represent alternate possibilities: First, other selective forces . . . may mask, modify, or interact with the selective action of cold temperature . . ." (Rand, incidentally, does not question my use of the theory of combined operation of additional selective factors; this is evident from the similarity between my comments quoted here and the concluding sentence to his paper (1961: 55), "More than one factor could be in operation at one time, working in different directions, canceling, or modifying each other.") Then, after citing some trends for intraspecific increase in wing length in the Sonoran region, I wrote (1958: 324) that "Finally, I find little evidence for the presence of Bergmann's rule, *per se*, within New World species." This sentence is ambiguous, open to misunderstanding, and seemingly in conflict with my comments elsewhere in the paper. The *per se* referred to the operation of Bergmann's rule without evidence of superimposed, additional selection pressures, and, thus, I feel that Rand is less than precise when he reports (1961: 46) my findings in the words "Hamilton, in 1958, writes that he can find little evidence for the application of Bergmann's rule (wing length and presumably body size being greater in colder climates) within New World species."

The few examples of larger wings and body weights in North American regions of low environmental temperatures, which Rand has listed, do not come to grips with the issue I raised in my paper, namely, that of the possible operation of additional selection pressures on wing length and body size in the southwestern region of North America. Nor do conclusions (Rand, 1961: 54) based on comparisons of the wing lengths and weights of populations from eastern and western United States provide a test for the validity of the aridity effect.

(2) Discussing the aridity effect, Rand states (1961: 54) that "On the basis of longer wing length of populations from the western part of North America, [Hamilton] postulated a greater body weight . . ." I find the first part of this quote puzzling since the aridity effect, as I formulated it, is a speculation (1958: 323) derived from intraspecific increase of wing length *in southwestern North America* (Sonoran region)—made clear by my comparison of these large winged Sonoran populations with conspecific populations from more northerly portions of western North America. A comparison of populations from eastern and western United States appears irrelevant to a critical analysis of the above problem. I present the following comments in complete agreement with Rand's statement (1961: 47), about equating wing length with weight, that "If accepted for

samples of birds of the same species from distant areas with widely different environments, there is danger of falling into grievous error."

To disprove the aridity effect, one would first have to demonstrate that such a tendency for intraspecific increase in wing length *and* body weight in the Sonoran region does not exist. Rand writes (1961: 54) "But, [Hamilton] had no weights." I had planned to delay further in reporting (manuscript in preparation) on the matter until I had adequate material to test the point in several species. The limited data available for *V. solitarius*, however, do support the postulated trend for Mexican increase in size (i.e., if we assume that body weight is a valid indicator of size). For example, consider the variation in three western races of *V. solitarius*: *cassinii*, *pinicolus*, and *repetens*. The distribution of these three breeding segments are, respectively and approximately, western United States, Sonoran Mexico, and southwestern Mexico. For males of the first race, Rand lists (1961: 51) values of 72 mm. and 15 grams; for the second race, there are available nine male specimens (Museum of Vertebrate Zoology: collected during June–July, 1957–1959, in the Sierra del Nido, Chihuahua) with average values of 82.7 mm. (81–85) and 18.0 grams (16.3–20.7); and, for the third race, two male specimens (Texas Cooperative Wildlife Collection) have August values of 81 mm. and 17.2 grams and 81 mm. and 19.2 grams.

How valid an indication of size body weight is, is still uncertain, and when more information about the variation in *V. solitarius* is available, my analysis of the variation may well be superseded. Any explanation, for the present, is hypothetical. For example, one might argue that populations of this species in Sonoran Mexico have longer wings and greater weights resulting from the operation of Bergmann's rule because of occupation of habitats in cooler, montane regions, but, then, this may not be the complete explanation since these populations appear to move south during the winter. One might also argue that populations of the *pinicolus* segment have increased wing lengths as a result of utilization of more open habitats, but, then, their body weights seem also greater than those of conspecific populations to the north in, say, Nevada, or to the northeast in eastern United States (see data for this species cited by Rand, 1961: 51). Finally, one could argue that populations of the *pinicolus* segment appear to have greater wing lengths, simply because the *cassinii* populations have smaller wing lengths in association with reduced body size as an auxiliary adaptation facilitating long-distance migration (for a discussion of such possibilities, see Hamilton, 1961, *Evolution*, 15: *in press*). However, this may not be the complete explanation since the *pinicolus* segment appears to consist of migratory populations which winter farther south in Mexico, where, apparently, occur resident populations of the *repetens* segment. In the light of such considerations, the aridity effect can only remain as previously presented—i.e., a speculation.

(3) Rand writes (1961: 52) that I state "that *Vireo olivaceus* and *V. griseus* show the tendency for insular populations to have 'greater wing length and relatively longer bill length (see Murphy, 1938).'" In reality, I stated (1958: 334) that "The strongly isolated, insular representatives of the Caribbean area show the tendency for insular populations to have greater wing lengths and relatively longer bill lengths (see Murphy, 1938)." The Murphy reference, as Dr. Rand states correctly, refers only to variation in bill length, and I regret not having made it clear that the citation in parenthesis refers only to the immediately preceding item (bill length).

I should like to add that for several years I have believed (without giving the matter much thought one way or the other) in the following theory: that there exists in some groups a tendency for insular populations derived from continents, or for populations of small islands derived from large islands, to acquire slightly greater wing lengths

(indicating, presumably, increases in size). For example, if one examines the data for variation in the superspecies *V. olivaceus* and *V. griseus* (Hamilton, 1958: 317, 325), it appears that the Caribbean populations tend to exhibit approximately equal or greater wing lengths than their superspecific counterparts on the adjacent American mainland. (The way Rand (1961: 52) lists my data for these two species prevents observation of this point.) Using my data for these two species, of the values (to the nearest 1.0 mm.) for the 12 Caribbean populations, five are larger, six are intermediate or equal, and one is smaller, when superspecific comparisons are made to the values and ranges of values for the American mainland, lowland populations (from Panama to Florida). The tendency among the vireos of the Caribbean islands to have increased wing length is, to me, unmistakable, provided one makes the comparison with adjacent mainland populations, from which the Caribbean ones are apparently derived.

It would be a good thing if others would take up the problem of the influence of insularity on wing length and size. Mayr and Vaurie (1948. *Evolution*, 2: 253–255, 260) have noted some evidence in the Dicruridae for a tendency of populations or isolates of small islands (12 of 17 cases for *Dicrurus leucophaeus* and *D. hottentottus*) to have greater wing lengths than conspecific populations of adjacent, larger islands. Among the passerine races endemic to Cozumel Island off Quintana Roo (see data of R. A. Paynter, Jr., 1955. The *Ornithogeography of the Yucatán Peninsula*), four seem larger (*Troglodytes musculus beani, Dumetella glabrirostris cozumelana, Cyclarhis gujanensis insularis*, and *Richmondena cardinalis saturata*), five are equal, and two appear smaller, when size comparisons are made to conspecific races on the adjacent mainland. However, absences of such a tendency can also be cited. Lack's data (1947. *Darwin's Finches*) for members of the Geospizidae, when arranged according to size of islands, seem not to show the tendency.

Discussing my data for populations of *Vireo* having breeding distributions in the Caribbean, Rand assumes (1961: 52) that the insular variation is due to "irregularity." He thus believes that my data do not demonstrate a "regularity," even though I reported only about "the tendency." While there can be no doubt that "irregularity" in some way is a component of character variation for any population or isolate, I am not willing to consider this as the only explanation for the variation in wing length of Caribbean vireos. My present stand on the matter (and I have no quantitative evidence for this) is that when continental populations reach small islands, a variety of centripetal selection pressures for specific niche or climatic adaptations may be relaxed, thereby permitting in time more general adaptations to be favored, involving, in some cases, increases in size. However, stringent competition can occur in the depleted or uniform habitats of small islands, and my comments refer mostly to pioneering populations exploiting previously vacant ecological niches and habitats.

(4) In conclusion, when I wrote my 1958 paper, I presented data in an attempt to unify the theories for ecogeographic variation in wing length and size in birds. That attempt leaves, admittedly, much to be desired, as does my current attempt (1961. *Evolution*, 15: *in press*). For example, the evidence for the aridity effect is still sparse and equivocal, and the evidence for the warm-humidity effect (op. cit.) can always be explained away as indicating an absence or reduction in operation of Bergmann's rule. The principal object of these two papers was to stimulate the collecting of new data and to propose new working models and alternate explanations, but not to disprove the work of others.—Terrell H. Hamilton. *Harvard Biological Laboratories, 16 Divinity Avenue, Cambridge 38, Massachusetts, 20 April 1961.*

ORNITHOLOGICAL NEWS

Dr. Oliver L. Austin, Jr., Curator of Birds, The Florida State Museum, has been appointed by the Nuttall Ornithological Club, Chairman of the Bent Life Histories of North American Birds Committee.

The Thirteenth International Ornithological Congress will convene at Cornell University, Ithaca, New York, from 17 to 24 June 1962.

The official announcement and application for membership in the Congress are now ready for distribution. Interested persons who have not already done so should send their names and addresses to the Secretary General as soon as possible.

A small fund has been obtained to provide partial support for the travel of a few persons coming from outside North America. Application forms will be sent to persons requesting them. (Citizens of the United States and Canada are not eligible.)

Before 1 December 1961, all applications for membership, travel grants, and places on the program should be returned to Charles G. Sibley, Secretary General, Fernow Hall, Cornell University, Ithaca, New York, U. S. A.

The Forty-third Annual Meeting of the Wilson Ornithological Society will be held at Purdue University in Lafayette, Indiana, from 6–8 April 1962.

NEW LIFE MEMBER

Hubert R. Doering, of Chicago, Illinois, a new life member of the Society, has been an active member since 1945. An account executive with D'Arcy Advertising Company, Mr. Doering is an amateur ornithologist whose interest began at the age of five when he attempted to hatch Bantam eggs. He then bred show-room poultry in a scientific manner, and now he is interested in population and life history problems, especially of warblers, owls, ducks, and geese. He has published an article on the birds of Bronxville, New York. In addition to being a member of the Wilson Ornithological Society, Mr. Doering is a member of the AOU, the Linnaean Society of N.Y., and numerous local groups.

ORNITHOLOGICAL LITERATURE

THE KIRTLAND'S WARBLER. By Harold Mayfield. Cranbrook Institute of Science, Bloomfield Hills, Michigan, 1960: 6¼ × 9¼ in., xvi + 242 pp., 8 pls., 9 figs., 44 tables, col. front. by Roger Tory Peterson. $6.00.

This long-awaited and excellent book provides our most complete account of the life of a wood warbler. It has, in addition, independent significance as a study of the history and present ecology of a small relict population of birds, and it will surely play an important part in the efforts of those whose duty it is to save the Kirtland's Warbler (*Dendroica kirtlandii*) from extinction.

Field work began over 30 years ago, when in 1930 Josselyn Van Tyne decided to study the Kirtland's Warbler. Among a number of ornithologists aiding him on occasion was Harold Mayfield, who participated in a trip in 1944 and thereafter collaborated as a full partner in the project until Van Tyne's death in 1957. The bird's breeding grounds were many miles distant from the homes of both investigators; the study required not mere field trips, but expeditions, and there was relatively little opportunity for sustained daily observation of individual birds or nests. To appreciate the difficulties, one might contrast the Kirtland's Warbler with the Song Sparrow (*Melospiza melodia*), for which, as a subject for her classic, Margaret Nice (1943. *Trans. Linn. Soc. N.Y.*, 6:1) listed these advantages: "it is abundant, thus affording many individuals for observation; it is widely distributed (having been available to me [at my homes]); it is easily watched, since it nests at our doorsteps and its territories are small; it readily enters traps, and can be easily reared by hand and kept in captivity." Lacking all of these advantages, Mayfield and Van Tyne nevertheless compiled remarkably voluminous data, and their project has succeeded. Direct evidence was sometimes difficult to accumulate on subjects requiring daily visits to the study area (e.g., duration of incubation, hatching sequence within the clutch, pair stability, and time required for mate replacement); but even on matters of this sort, skillful analysis of fragmentary data has yielded Mayfield much circumstantial evidence to throw light on the direct observations.

There is in the book a natural emphasis on ecology, and the opening chapters on the known history of the Kirtland's Warbler and on the summer and winter habitats are of great interest. So restricted is the species' breeding range in Michigan that no nest has ever been found more than 60 miles from the place in which Norman Wood discovered the first, in 1903. Equally limited is the seral stage of vegetation inhabited: small jack pines (*Pinus banksiana*), springing up in clumps a few years after forest fires, are the dominating feature, for a brief period (typically 10 to 12 years), of the requisite plant association; then the trees become too large, the openings between them close, lower branches are shaded out, and the warbler leaves. There are still further requirements, that the burned-over tract be extensive enough to attract and accommodate the cluster or colony of territories which the males establish, and that the soil be sufficiently porous to drain off surface water before the nests depressed in the ground are injured. Thus, although the jack pine is widely distributed in northern North America, Mayfield believes that the reason the bird breeds only in Michigan is that only there has there been, *continuously*, the required combination of highly specialized conditions. The period of greatest abundance of the Kirtland's Warbler, since it entered the state in the wake of jack pines spreading northward as the Wisconsin glacier retreated, he puts in the 1880's and 1890's. Since that time of forest fires and extensive burning following early timber cutting, numbers of the Kirtland's Warblers declined to fewer

than 1,000 in 1951. For the future of the habitat Mayfield finds "no immediate cause for alarm" (p. 28), but a subsequent chapter on population dynamics suggests little reason for optimism about the prospects for the species itself.

Why this narrow restriction as to habitat? The Kirtland's Warbler seems not to be a food specialist, limited by the distribution of organisms comprising its diet. Part of the answer to the question, Mayfield believes, is a high degree of vulnerability to nest predators as the result of an exceptionally long incubation period, 14 days as compared with from 11 to 13 days for other open-nesting parulids. A general unwariness in adults he thinks may put an additional premium on sanctuary, and there is a suggestion that the bird does not prosper against competition. In any event, pine barrens provide greater immunity from predators and isolation from competitors than does deciduous scrub; and it is pointed out that once the species became restricted to jack pines a high precision in orientation may have been an obstacle to potential dispersal into new habitat.

Of that portion of the work, about half of it, devoted to breeding behavior and biology, little summary is needed. The stages of reproduction and of development of the young are treated consecutively, with separate chapters on voice and on weights and plumages. The description of adult behavior surpasses in comprehensiveness any in the literature on parulids, while one seldom sees for a perching bird so detailed an account of intra-family relations and the development of fledglings in the period between nest-leaving and independence. Data on matters of breeding biology have been subjected to rigorous standards of exclusion, and this fact and the meticulous attention to definition of terms and conditions of observation assure the lasting utility of the book as a source.

The longest chapter in the book is devoted to the relations between the warbler and a serious, perhaps the most serious, enemy, the Brown-headed Cowbird (*Molothrus ater*). This material will be an important reference for students of the latter species and of brood parasitism. Although the rate of parasitization of Kirtland's Warbler nests, about 55 per cent, is paralleled or surpassed in the cases of populations of a few other hosts, Mayfield makes a convincing argument that no other *species* is known to suffer comparable pressure. Considering the factor that is ultimately decisive, i.e., loss in net annual production of young, if the Kirtland's Warbler were unmolested by the cowbird, as it probably was until the 1870's, it would bring off 60 per cent more fledglings. This conclusion is supported by analysis of losses, stage by stage, in parasitized nests as compared with nests containing only host eggs. The chapter also contains contributions on the cowbird's selection of nests in which to lay, and on other aspects of its behavior in connection with laying.

The final substantive chapter is a population study. Equally as interesting as the conclusions presented is a novel method of using fragments of data on reproductive success. These data are first presented conventionally, but there is recognition of the error of arriving at hatching or fledging percentages from nests discovered after the incubation or nestling periods have begun; and the sample of nests observed from the laying of the first egg until the fate of the nest was determined was too small to be used. Mayfield is able, however, to determine rates of loss *per day* at each stage of development until fledging and thus to derive the probability of success of nests and eggs in a hypothetical sample. Further, the number of nests and eggs produced by a large sample of pairs can be predicted, and these figures when combined with those on success yield a hypothetical annual rate of production, which proves to be 1.4 fledglings per pair of adult warblers. The complexity of the calculation will be apparent upon consideration that many factors (e.g., probability of renesting, clutch size) are constantly

varying as the nesting season advances; and there are other difficulties to be taken into account. I thought the reasoning logical and clear.

Survival of adults is at the rate of about 60 per cent per year, so that the remaining life expectancy of an adult in June is about two years. The conclusion is based on returns of banded birds; there is the usual assumption that the annual mortality rate is unaffected by age. Given the accuracy of the calculated rate of production of fledglings and of that of adult mortality, the rate of survival of fledglings to the following breeding season would have to be 57 per cent to maintain the population. In fact, as Mayfield makes clear, it is most unlikely that so high a percentage of young survives this period. Therefore Kirtland's Warbler numbers may be declining. Undoubtedly there will be more to say on this subject after Mayfield completes his second decennial census of the population, during the present summer.

The book concludes with a list of "Problems for Further Study," which will be useful to future students of the species, but it is one of the merits of the work that his familiarity with the literature and with current problems enables Mayfield to raise many interesting and unanswered questions throughout the report. In this respect he fulfills the functions of a good teacher as well as those of a model.

On points of form and format, the volume can be enthusiastically endorsed. It is well written, attractively bound, and free from errors. The index is a little too general to lead to some subjects with maximum speed and not quite imaginative enough to refer to all pages on which appears material possibly relevant to various indexed words. However, sub-headings within each chapter and summaries at the end compensate for this shortcoming and add much to the convenience of use. In sum, this is a fine and important book, and it deserves hearty recommendation.—Val Nolan, Jr.

The Wonders I See. By John K. Terres. With drawings by Walter Ferguson. J. B. Lippincott Company, Philadelphia and New York, 1960: 5¾ × 8¼ in., 256 pp. $5.00.

People who like *Audubon Magazine* may be expected to enjoy this collection of nature sketches—and not surprisingly, since the author of the book was an editor of that magazine for eleven years.

The book consists of 84 selections, nearly half of them about birds. The rest touch on a variety of subjects, particularly insects, mammals, and conservation. Included are original observations, explanations of puzzling questions, retelling of historical events, and personal comment. These jottings range in length from one paragraph to eight pages. They are arranged according to the time of year, and each begins like an entry in a field journal, with date, location, and weather. Since the parts are mostly short and unrelated to the others in sequence, a reader is likely to pick up the book and read it a little at a time rather than continuously from cover to cover.

Examples of items especially interesting to bird students are the following: "Why Don't Birds' Feet Freeze in Winter?" "The Great Lapland Longspur Tragedy," "Why Does the Mockingbird 'Flash' Its Wings?" "How the Cattle Egret Got to America," "When Do Birds First Learn Fear?" "The Mystery of Bird 'Anting,'" "McAtee: Food Analyst of the Birds," and "Where Do Birds Sleep at Night?"

The treatment of subjects is factually accurate but simple enough to be within the comprehension of an interested child. (Words such as "mammalogist" and "gestation" are defined.) A book of this kind intended for recreational reading inevitably will be judged in part for its literary quality, and I think it is fair to say that a person with an

ear sensitive to grace and elegance of expression will find passages to criticize. Most readers who share the author's enthusiasm for nature, however, will not be severe in their literary judgments of this work.—HAROLD MAYFIELD.

DICTIONARY OF WORD ROOTS AND COMBINING FORMS. By Donald J. Borror. N-P Publications, Palo Alto, California, 1960: 5 × 7 in., v + 134 pp. Stapled in stiff paper cover. $2.00.

This modest publication is aimed at "the beginning student [of biology], the medical student, and the taxonomist." The introduction contains general directions for the use of the dictionary, plus a handy set of rules for the pronunciation of scientific names (I have more than once found myself conversing with a colleague who pronounced some scientific name so differently from my own concept of its pronunciation that I failed at first to understand what animal he was discussing, and neither of us certain as to who was correct).

The body of the work is an alphabetical list of word roots, prefixes, and suffixes, mostly derived from Latin and Greek but with a few words that have found their way into scientific nomenclature from other languages—and even from onomatopoeia, as in "phoebe (from its call). The phoebe." There follows a very brief guide to the formation of scientific names of plants and animals, and a list, classified by subject (colors, habitats, structures, etc.), of common combining forms intended as a help in selecting roots for the formation of new names.

This booklet (for it is scarcely more than such) will probably be most useful as an introduction to word meanings for the beginner who does not intend to pursue the subject at any length. There are several more complete publications of this nature, which Borror's book will not replace. I myself use "Composition of Scientific Words," by Roland W. Brown of the U.S. Geological Survey (published by the author, 1956: 882 pp.), which is about as complete a guide to word formation and derivation as one could wish for. Brown's book, unlike Borror's, has the advantage of having the classical roots and English words cross-referenced in the same glossary. Thus, Borror gives "anas (L). A duck." while Brown gives "**anas**, L. duck; *anaticula*, dim., duckling; *anatinus*, of ducks; see **duck**." Under **duck** we find no less than eleven Greek and Latin words which were applied to various kinds of ducks, together with examples of the use of each word or root in a scientific name: "L. *querquedula*, f. a kind of duck: *Querquedula cyanoptera* (cinnamon teal)."

The modest price will permit wide distribution of Borror's little book, but the serious student of nomenclature and the practicing taxonomist with a continuing need to coin new names will wish to own a more complete work.—KENNETH C. PARKES.

THE TRUMPETER SWAN: ITS HISTORY, HABITS, AND POPULATION IN THE UNITED STATES. By Winston E. Banko. U. S. Department of the Interior, Fish and Wildlife Service, North American Fauna No. 63, 1960: x + 214 pp., 6 × 9⅛ in., front., 54 figs. (including photos., drawings, and maps), 16 tables. Paper covered. $1.00.

This publication will appeal to everyone interested in birds, from bird lovers to professional management personnel. Its wide appeal is due to a broad approach which includes historical, behavioral, and statistical data, all arranged in a logical fashion and presented with extraordinary clarity. An abundance of remarkably fine photographs by Banko and others provide the best illustrations of Trumpeter Swans that I have seen. The

text is further enlivened by a series of crisp line-cuts by Shirley A. Briggs. This is a successful monographic treatment of a single species, although the omission of much Canadian data (a separate study by Ron H. Mackay of the Canadian Wildlife Service is in progress) is unfortunate. Still, the status of Trumpeter Swans in Canada is briefly sketched and reference is made to most published Canadian reports. Saskatchewan birders, however, will be disappointed to learn that their province is omitted in the discussion of recent breeding records in Canada (see *Blue Jay*, 1953, 11: 26–27).

The author states in the foreword: "This account includes a historical record of this bird in the United States and Alaska, an outline of its habits and characteristics in its native Rocky Mountain environment, and furnishes information necessary to guide its future." The Trumpeter Swan is introduced as a member of a group of birds (i.e., swans) which have played a prominent role in human history and which have long been admired for their grace and beauty and large size. Their systematic position is also presented. The occurrence of the Trumpeter Swan in North America from the ancient past, through pioneer days and up to 1957, is well documented in a chapter headed: "Distribution and Status." This section includes accounts of the marketing of swan skins by the thousands, an activity which apparently was a major factor in the near extinction of the trumpeter. Strangely, it is evidently not even clear what use was made of these skins! Admirers of Sir John Richardson will be pleased to note from the historical section that he was the first to describe a positive method of differentiating the Trumpeter Swan from the Whistling Swan. The tracheal anatomical difference which he discovered is still the only reliable character. Ecological aspects are considered in the chapter on "Habitat" and include discussions of the former general environments and, specifically, characteristics of the swan's breeding grounds at Red Rock Lakes Refuge. Although it formerly occurred as a breeding species across the continent and throughout several life zones, its ecological niche is shown to be very limited. Both summer and winter habitat requirements are described.

The "Life Cycle" section includes a useful description of the Trumpeter Swan and comparison with the similar Whistling Swan. The difficulty of using bill coloration to separate these species is pointed out. I was surprised to learn that the reddish streak on the bill of the Trumpeter Swan is "confined almost wholly to the basal section of the lower mandible edge . . ." Delacour (1958. The Waterfowl of the World. Vol. 1) states: "The massive bill is wholly black except for a narrow red border to the anterior part of the upper mandible." Peter Scott's accompanying illustration, however, favors Banko's description. According to Banko, not even this character is consistent.

The behavior notes constitute an important contribution to our knowledge of this species. Observations of several displays are described briefly and directly and are illustrated by good photographs. I cannot wholly agree with Banko that analysis of displays "should await that time when extensive recordings of their vocal efforts have been made in synchronization with motion pictures of their various actions." This may be very desirable but in the interim I think it would be useful to proceed as we can. The behavior observations reported by Banko might have been described in more detail and a greater attempt might have been made to relate displays to function. Although there is a considerable discussion of territorialism, the size of the territory is not quite clearly stated, apparently because of the effect of irregular habitat, although maximum area available is reported as from 70 to 150 acres per nesting pair.

Information on the "Life Cycle" also includes breeding data, nesting habits, development of the young, feeding habits and food, and a discussion of limiting factors and longevity. In spite of the lengthy list of mortality factors of natural origin, man may

still be considered the most significant limiting factor. However, man's recent activities on behalf of the Trumpeter Swan have clearly been of benefit to the species. Banko estimates the total continental population of Trumpeter Swans now at probably 1,500 or more. A detailed analysis of Trumpeter Swan population dynamics is presented which will be of interest to students of natural populations. The data concern chiefly the population of Red Rock Lakes and Yellowstone Park, both of which were carefully censused annually over a 27-year period. It is shown that a saturation point was reached and that breeding productivity was depressed at this time through a decline in cygnet production. In broader terms the rate of productivity of mated pairs varied inversely with changes in population density. The data to support these conclusions are very clearly presented in table and graphs, but, as the author indicates, the exact mechanism affecting cygnet productivity is not known. Since maximum populations appear to have been attained on the present refuges, Banko concludes that it is highly desirable to keep close check on isolated breeding areas and to make further efforts to establish wild populations in suitable areas within the former known breeding range of the species. He says: "It is the objective of the Bureau [U. S. Fish and Wildlife Service] to maintain the wild population of these rare fowl at an optimum level—the greatest number which can be consistently supported in their natural environment."

An extensive bibliography supports the work and the index appears to have been carefully prepared. Proofreading seems to have been thorough. The U. S. Fish and Wildlife Service and Winston Banko deserve congratulations for this successful exposition of a remarkable species.—Robert W. Nero.

The Audubon Book of True Nature Stories. Selected and edited by John K. Terres. Thomas Y. Crowell Company, New York, 1958: 6 × 9½ in., x + 294 pp. Illustrated by Walter W. Ferguson. $5.00.

This is Nature: Thirty Years of the Best from *Nature Magazine*. Selected and edited by Richard W. Westwood. Thomas Y. Crowell Company, New York, 1959: 7 × 10¼ in., x + 214 pp. Illustrated by Walter W. Ferguson. $5.95.

The selections in both of these books are entertainingly informative and just the right length for "pick-up" reading. Those in "The Audubon Book," all from *Audubon Magazine*, deal mostly with birds and mammals, particularly their relationships to human beings, while those in "This is Nature" cover a wider variety of topics ranging from boulders deposited by glaciers, sight and hearing, pollen, and mangroves to turtles, seahorses, prairie dogs, and Snowy Owls. The charm of both books is greatly enhanced by Walter Ferguson's sensitive drawings. "This is Nature" is further embellished with photographs.—Olin Sewall Pettingill, Jr.

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A WORD TO MEMBERS

The Wilson Bulletin is not as large as we want it to be. It will become larger as funds for publication increase. The Society loses money, and the size of the *Bulletin* is cut down accordingly, each time a member fails to pay dues and is put on the "suspended list." Postage is used in notifying the printer of this suspension. More postage is used in notifying the member and urging him to pay his dues. When he does finally pay he must be reinstated in the mailing list and there is a printer's charge for this service. The *Bulletin* will become larger if members will make a point of paying their dues promptly.

NOTICE OF CHANGE OF ADDRESS

If your address changes, notify the Society immediately. Send your complete new address to the Treasurer, Merrill Wood, Dept. of Zoology and Entomology, Frear Laboratory, Pennsylvania State University, University Park, Pennsylvania. He will notify the printer.

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